THE UNIVERSITY OF ALBERTA

DISPERSION AND DISPERSAL OF FEMALE AND JUVENILE FRANKLIN'S GROUSE IN SOUTHWESTERN ALBERTA

BY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Dispersion and Dispersal of Female and Juvenile Franklin's Grouse in Southwestern Alberta" submitted by Kenneth Hubert McCourt in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Dispersion and dispersal as well as several other aspects of the biology of female and juvenile spruce grouse (Canachites canadensis franklinii) were studied in southwestern Alberta during the summers of 1965-1968.

A technique was developed for distinguishing adult from yearling females based on shaft diameter and total length of the following feathers: first primary, a central upper tail covert, and a central rectrix. Approximately 37% of the spring population of females were yearlings. Nearly all new females entering the population were yearlings.

Comparisons of home range sizes indicated that yearling females utilized a larger area than adults.

A technique for determining the age of juvenile spruce grouse was developed based on measurements of their juvenal and postjuvenal primaries. Using this method to determine the chronology of reproductive events, it was found that most laying began between May 28 and June 11. During the study, 77% of the clutches hatched between June 28 and July 11. Approximately 50% of the females were successful at raising a brood. There was evidence that yearlings were less successful at raising broods than adults. Yearling females were not as closely associated with territorial males as were adult females.

The study area included lodgepole pine forest (71.5%), poplar and mixed forest (17.5%), relict spruce forest (3.5%), and meadow and marsh (7.5%). Female spruce grouse were observed with few exceptions in the pine forest of which they used

but 40%. In that portion of the pine forest inhabited by grouse, the average canopy coverage of overstory was greater and middlestory less; height, diameter, and density of trees were greater; and slope of the terrain was less steep than in the unoccupied area. Within the inhabited area, females seen during the breeding period selected cover which was not very different from that which was present on the average over the area occupied by grouse. Females seen during the summer with broods selected a relatively light overstory and a relatively heavy middlestory compared to that selected during the breeding period. Females without broods seen during the summer selected cover which was heavier at both overstory and middlestory levels than during the breeding period.

Juveniles were the main segment of the population involved in dispersal. Of the banded female juveniles, 14% were seen on the study area in a subsequent year. Of the banded male juveniles, 43% were seen on the study area in a subsequent year.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Dispersion and dispersal of female and juvenile Franklin's grouse (*Canachites canadensis franklinii*) were studied in southwestern Alberta in the summers of 1965 through 1968.

Several studies of dispersal in grouse have shown that juveniles tend to disperse widely between their first and second summers, and subsequently become localized on a territory or home range, with females being less stationary than males. Chambers and Sharp (1958) and Hale and Dorney (1963) working with ruffed grouse (*Bonasa umbellus*), and Mussehl (1960), Boag (1966), and Bendell and Elliott (1967) working with blue grouse (*Dendragapus obscurus*), have shown this to be the case. Choate (1963) showed that in white-tailed ptarmigan (*Lagopus leucurus*), more males than females raised on his study area returned to it, that adult females occasionally returned to the same breeding areas, and that adult males showed fidelity to a territory between years. Territorial behavior in males during the breeding season also accomplished a pattern of dispersion of males in rock ptarmigan (*Lagopus mutus*), and willow ptarmigan (*Lagopus lagopus*) (Weeden, 1963); in red grouse (*Lagopus lagopus scoticus*) (Jenkins *et al*., 1963 and 1967); and in blue grouse (Blackford, 1958; Boag, 1958; and others).

The importance of habitat selection on the dispersion of male grouse has been noted in red grouse by Jenkins *et al*. (1963 and 1967); in ruffed grouse by Dorney (1959), Gullion

et al. (1962), and Palmer (1963); and in blue grouse by Boag (1966), Elliott (1965), and Bendell and Elliott (1967).

Wynne-Edwards (1962) presented an hypothesis which states that intraspecific interactions affecting dispersion act to regulate population numbers. His arguments, as far as grouse are concerned, are based on the male segment and most of his evidence comes from studies of the monogamous *Lagopus* species. In his discussion of lek species, the prairie-chicken (*Tympanuchus cupido*), sharp-tailed grouse (*Pedioecetes phasianellus*), and sage grouse (*Centrocercus urophasianus*), Wynne-Edwards admitted, in the absence of more definite evidence, he could only surmise that when there is a surplus of females the number of matings is controlled by males. In red grouse, Jenkins *et al*. (1963 and 1967) and Watson (1967) showed that territorial behavior sets a limit to the numbers of individuals able to hold a territory during the winter and thus to the subsequent breeding stock. Wynne-Edwards did not indicate how territoriality in males could regulate population numbers in a polygamous non-lek species. Bendell and Elliott (1967) concluded that territorial behavior in male blue grouse did not regulate breeding density but functioned mainly to provide an area for males to attract a mate, court, and copulate free from interference from other birds. Boag (1966) pointed out that because of the promiscuous breeding habits exhibited by blue grouse, a limitation on the number of adult males would not influence population growth. It follows that factors governing dispersion of females, especially in a polygamous non-lek species, may be

important in population regulation.

Stoneberg (1967) treated dispersion of female Franklin's grouse only superficially, concluding that on his study area home ranges of adult females coincided with those of resident males. In blue grouse, Elliott (1965) and Lance (1967) investigated female dispersion more fully and arrived at the conclusion that females are attracted to males during the breeding season but are unaffected by intraspecific interaction after this period. Brander (1967), using radiotelemetry, concluded that female ruffed grouse were attracted to drumming males. Several authors have indicated that dispersion of female grouse with young broods is related to openings in forest cover with an abundance of ground vegetation. Stewart (1956) and Sharp (1963) suggested this in ruffed grouse, Mussehl (1963) showed such a relationship in blue grouse, and Stoneberg (1967) indicated a similar situation in Franklin's grouse. Apart from these studies, few investigators have considered the problem of female dispersion in polygamous non-lek grouse.

The primary objectives of this study were to attempt to describe and explain dispersion and to discover some of the properties of dispersal in the female and juvenile segments of a population of Franklin's grouse. As there has been very little information published on this species, data on several aspects of its basic biology were gathered. Factors dealt with that could have an effect on dispersion were age of the grouse, stage of reproductive cycle, intraspecific interaction,

vegetation, and topography.

METHODS

Research was begun in early May and terminated in late August or early September of 1966, 1967, and 1968 after an initial investigation of the area in the summer of 1965 indicated that a study was feasible. This research was done in conjunction with that carried out by R. A. McLachlin concerning the male portion of the same population (in prep.). Through cooperation, an increased amount of data were collected. MacDonald's (1968) study of courtship and territorial behavior of Franklin's grouse was conducted on a part of the study area during the breeding season from 1963 to 1967.

Each summer two to four persons searched systematically for grouse on a daily basis. The method of search involved selecting a naturally bounded block of the study area and walking back and forth across it in an attempt to cover as much area as evenly as possible.

Dogs were used by McLachlin as an aid in finding grouse in 1966 and 1967. A systematic search over the entire study area in 1966 revealed that certain areas were uninhabited by spruce grouse. Thereafter, in order to increase the number of observations of birds, search efforts were concentrated in areas known to be suitable for grouse. However, each year the area thought to be uninhabited by grouse was periodically searched to determine whether grouse were utilizing the area.

Every unbanded grouse found other than young chicks was captured by means of a snare on the end of a 20 foot telescoping fibre glass pole (Zwickel and Bendell, 1967). Small chicks were captured by hand or with a butterfly net until approximately two weeks of age after which time they were snared with the noosing pole.

Captured birds were individually marked with colored leg bands to permit recognition of individuals in the field. A numbered aluminum band with a return address on it and of a color distinctive for the year was put on the right leg and a maximum of three more bands, a total of two per leg, were used to obtain an individual color combination. Some young chicks were marked by loosely tying thin strips of elastic seismic tape around the legs to obtain individual color combinations. Distinctive combinations of claws were clipped on others. All chicks seen after they were about six weeks old were banded with regular bands. At about this age the sex of the bird could first be determined by examination of the lateral breast feathers and central rectrices. Adult and yearling females could easily be distinguished from males since the plumage of Franklin's grouse is strikingly sexually dimorphic.

The date, time of day, and location were recorded when grouse were captured or recaptured. The latter was recorded as coordinates, read to the nearest millimeter, from large gridded aerial photographs of the study area. These photographs of which the scale is 1 cm to 44.8 m were expanded

from photographs with a standard scale notation of 1:1,320 taken in 1957.

The weights of adults and yearlings were determined with spring scales and recorded to the nearest 5 grams. Chicks were weighed to the nearest gram.

The primary feathers of all birds were measured to the nearest millimeter. The first (proximal) primary was measured from the point of insertion in the skin to the tip. All others were measured by sliding a ruler along the proximal edge of the feather being measured until it fitted snugly against the skin between the feathers.

No reliable techniques for aging Franklin's grouse had been published when this study was begun. A tenth and first primary, central rectrix, and upper tail covert were plucked from each captured bird. Of the three latter feathers, measurements of the diameter of the rachis at the superior umbilicus in the same plane as the vane were taken to the nearest 0.1 mm with Vernier calipers. The length of these straightened and flattened feathers from the inferior umbilicus to the tip of the vane was measured to the nearest 1.0 mm.

In addition, associations with other spruce grouse were noted, presence or absence of brood patch was recorded from adult and yearling females, broods were counted when present and other miscellaneous field notes were taken.

At subsequent observations of marked birds, only some of the above data were collected.

At observation sites of birds, vegetation analyses were

done. Vegetation was arbitrarily divided into three layers: overstory - trees which reached breast height and above; middlestory - shrubs over 25 cm but under breast height; and understory - all plants under 25 cm high. One exception to this classification was that even though alder (Alnus crispa) was sometimes above breast height, it was always classed as middlestory. Using the position at which the bird was first seen as a centre for a circular plot containing 50 m^2, the amount of cover provided by species and by total vegetation in the overstory and middlestory were estimated using a modification of Daubenmire's (1959) scale of values:

Coverage class	Range of coverage
0	absent
1	present to 5%
2	>5% to 25%
3	>25% to 50%
4	>50% to 75%
5	>75% to 95%
6	>95% to 100%

In order to characterize the study area in terms of vegetation and to compare vegetation utilized by birds with that which was available, vegetation analyses similar to those done at locations where birds were sighted were done at random over the study area. These sites were selected from the gridded study area by means of a table of random numbers. As well as recording canopy coverage at these random plots, overstory canopy height, tree diameters at

breast height, and density of trees in the overstory were recorded. The slope was measured at these sites with an Abney level, an instrument used also to determine canopy height.

Statistical tests used included the t-test and Chi-square for independence (Steel and Torrie, 1960). The five per cent level was considered statistically significant.

DESCRIPTION OF THE STUDY AREA

The study area was located near the R. B. Miller Biological Station which is situated at the confluence of the Sheep River and Gorge Creek in southwestern Alberta. Figure 1 shows the location of the study area.

The study area was composed of the main study area - 600 ha in size, and the auxiliary study area - 1,200 ha in size. While field work was concentrated on the main study area, some time was spent on the auxiliary study area to band birds in an effort to determine the extent of movement on and off the main study area. In 1965, only part of the main and auxiliary study area was used.

The elevation of the main study area ranges from 4,900 feet to 6,000 feet. The forest cover, influenced by extensive fires in the 1930's, consists mainly of thick stands of lodgepole pine (Pinus contorta) of almost uniform age. Interspersed within the pine forest are clumps of trembling aspen (Populus tremuloides) and balsam poplar (Populus balsamifera);

low open marshy areas and grassy meadows; and islands of white spruce (*Picea glauca*) which survived the fires.

The vegetation was grouped into four main types: lodgepole pine forest, poplar and mixed forest, relict spruce forest, and meadow and marsh. The extent of these vegetation types over the main study area was roughly determined from aerial photographs (Table 1).

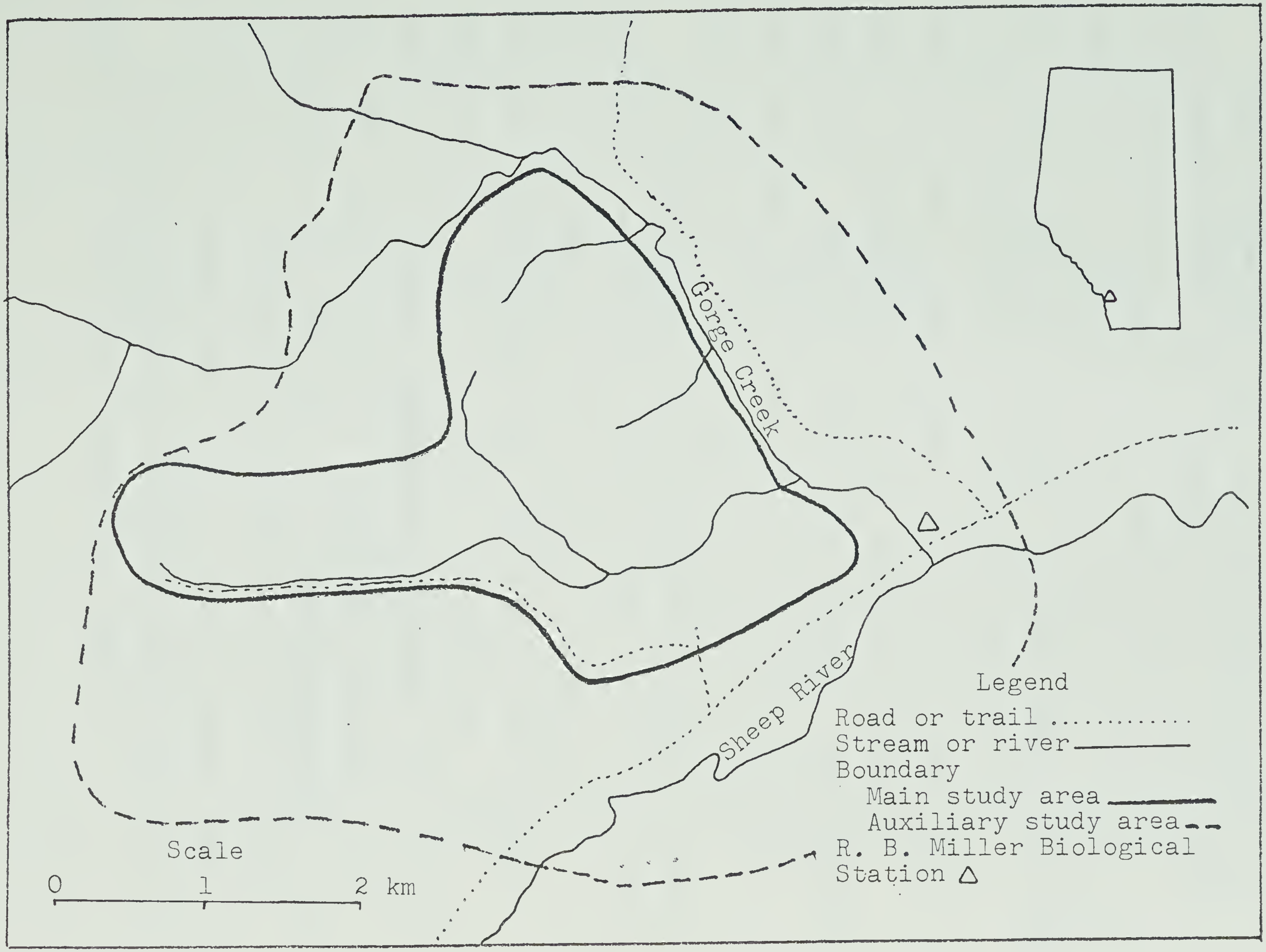
Table 1. Extent of four vegetation types on the main study area based on aerial photographs taken in 1957.

Vegetation types	Area in ha	Per cent of total area
Lodgepole Pine Forest	429.5	71.5
Poplar and Mixed Forest	104.5	17.5
Relict Spruce Forest	21.0	3.5
Meadow and Marsh	45.0	7.5

The extent of different forest types in 1957 probably did not differ significantly from their extent during this study.

The characteristics of each forest type will be described by using the results of 310 random vegetation analyses. These results have been kindly made available to me by R. A. McLachlin. The data will be used to compare with vegetation analyses done at sites where grouse were seen. Because of this and to show that there was a great deal of variation in the characteristics of the vegetation on the study area,the description of it will be rather detailed.

Figure 1. Location of the main and auxiliary study areas.


Gorge Creek
Sheep River
Legend
Road or trail
Stream or river
Boundary
Main study area
Auxiliary study area
R. B. Miller Biological Station
Scale
0
1
2 km

Lodgepole Pine Forest

Table 2 shows the number of cover values recorded for each species and the total vegetation in the overstory and middlestory of 225 random plots within the pine forest. Lodgepole pine was present in 99% of the overstory plots, and had a modal cover value of three. The most common cover value of white spruce, present in 53% of the plots, was one. Trembling aspen, balsam poplar, and willow occurred infrequently, being present in 3%, 3%, and 25% of the plots, respectively. When all species were combined, some overstory cover was present in all but one of the plots. The most common cover value for all species together was three.

In the middlestory, the most important species in terms of frequency were willow, present in 64% of the plots; alder, 45%; and white spruce, 43%. In order of frequency of occurrence, the following other species were also present: lodgepole pine, 15% of the plots; rose (Rosa sp.), 15%; Canadian buffalo berry (Shepherdia canadensis), 8%; trembling aspen, 7%; shrubby cinquefoil (Potentilla fruticosa), 3.5%; balsam poplar, 3%; and dwarf birch (Betula glandulosa), 1.5%. Middlestory cover was present in 92% of the plots, with one as the most frequent cover value of all the species combined.

The diameter measurement (DBH) and density data for the trees on the 225 plots are presented in Table 3.

Table 2. Number of cover values for individual and combined species in the overstory and middlestory on 225 random plots within a lodgepole pine forest.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	3	-	-	-	-	-	-	-	-	5
4	-	42	-	-	-	-	-	-	-	-	53
3	2	93	-	-	-	-	-	-	-	-	89
2	29	70	1	2	1	-	-	-	-	-	67
1	89	15	5	2	54	-	-	-	-	-	10
0	105	2	219	221	170	-	-	-	-	-	1
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	3	-	-	-	-	6
3	1	-	1	-	2	10	-	-	-	-	25
2	5	3	-	2	16	32	2	1	1	5	63
1	87	32	7	14	126	56	1	2	32	14	113
0	132	190	217	209	81	124	222	222	192	206	18

* 6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1= present - 5%, 0= absent.

Table 3. Stem density by diameter class (DBH) of the overstory tree species in 225 random, circular plots (50 m^2 each) within the lodgepole pine community type.

Diameter class(cm)	Number of individuals in each diameter class					Grand Total
	Picea glauca	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix* sp.	
18-20	1(<1)[a]	4(<1)	-	-	-	
16-18	-	9(<1)	-	-	-	
14-16	-	59(1)	-	-	-	
12-14	1(<1)	69(1)	-	-	-	
10-12	1(<1)	306(7)	-	-	-	
8-10	2(<1)	709(16)	-	-	-	
6- 8	10(3)	843(20)	-	4(31)	2(<1)	
4- 6	26(8)	834(20)	-	2(15)	11(2)	
2- 4	120(36)	845(20)	1(17)	1(8)	70(18)	
0- 2	174(52)	637(15)	5(83)	6(46)	326(80)	
Total	335(100)	4,315(100)	6(100)	13(100)	409(100)	
Stems/ha	298(6.6)[b]	3,836(85.0)	5(0.1)	12(0.3)	364(8.0)	4,514(100)

[a] % of Total

[b] % of Grand Total

Seventy-six per cent of the lodgepole pine stems had diameters in the 2 to 10 cm range. Most of the white spruce and willow stems were small, with at least 90% of the stems being 4 cm or less. Since balsam poplar and aspen were present in so few plots, data on their diameters are probably not very meaningful.

The figures on density show that lodgepole pine composing 85.0% of the total trees is the dominant species in the overstory. Mean canopy height of the overstory was 7.3 ± 2.1 m with a range of 0-13 m. The average slope of the ground on the 225 plots was $9.2 \pm 5°$ with a range of 0-33°.

The understory vegetation in the lodgepole pine forest was sparse in the spring and often covered by snow. The first green plants to be seen in the understory, besides the trees and shrubs too small to be counted as middlestory, were mosses, twinflower (Linnaea borealis), bear berry (Arctostaphylos uva-ursi), bunchberry (Cornus canadensis), wintergreen (Pyrola sp.), blueberries (Vaccinium spp.), and pussytoes (Antennaria spp.). In summer, aster (Aster sp.), heart-leaved arnica (Arnica cordifolia), strawberry (Fragaria virginiana), fireweed (Epilobium angustifolium), hedysarum (Hedysarum sp.), coltsfoot (Petasites palmatus), Indian paint brush (Castilleja miniata), northern bedstraw (Galium boreale), wild sweet pea (Lathyrus ochroleucus), and wild vetch (Vicia americana) became common as well. By this time too, pine grass (Calmagrostis rubescens) was present in almost every plot where vegetation analyses were done.

<u>Poplar and Mixed Forest</u>

Table 4 shows the number of cover values recorded for each species and the total vegetation in the overstory and middlestory of 46 random plots within the poplar and mixed forest. In the overstory, white spruce was present in 80% of the plots, lodgepole pine in 61%, balsam poplar in 47%, aspen in 52%, and willow in 28%. The most common cover value for each of these species was two. Overstory cover was present in 98% of the plots, with 85% of the total cover values being either two or three.

In the middlestory, only willow, on 72% of the plots, and white spruce, on 63% of the plots, were common. Middlestory cover was present on 96% of the plots. The most common cover value was two. The DBH's and densities of trees in the 46 plots within the poplar and mixed forest are presented in Table 5.

The stems of lodgepole pine were about the same size as in the pine forest type. Seventy-three per cent were between 2 and 10 cm in diameter. The stems of willow and white spruce were also mostly small as in the pine forest. Balsam poplar and aspen were present in greater numbers in the poplar and mixed forest type. Half of the aspen were over 4 cm in diameter and over half of the balsam poplar were over 2 cm in diameter.

Although both white spruce and lodgepole pine were present on more plots than either balsam poplar or aspen, the deciduous trees outnumbered the conifers. This demonstrates

Table 4. Number of cover values for individual and combined species in the overstory and middlestory on 46 random plots within the poplar and mixed forest.

Cover value *	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	1
4	-	1	-	1	-	-	-	-	-	-	2
3	1	1	3	4	1	-	-	-	-	-	20
2	18	21	13	14	4	-	-	-	-	-	19
1	18	5	6	5	8	-	-	-	-	-	3
0	9	18	24	22	33	-	-	-	-	-	1
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
3	-	1	-	-	1	-	-	-	-	-	5
2	3	-	1	-	15	4	-	-	-	2	27
1	26	8	12	12	17	7	1	2	5	6	13
0	17	37	33	34	13	35	45	44	41	38	1

* 6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1= present - 5%, 0 = absent.

Table 5. Stem density by diameter class (DBH) of the overstory tree species in 46 random plots within the poplar and mixed forest community type.

Diameter class (cm)	Number of individuals in each diameter class					Grand Total
	Picea glauca	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix* sp.	
16-18	-	1(1)	-	-	-	
14-16	-	3(2)	-	-	-	
12-14	-	9(6)	-	2(1)	-	
10-12	-	19(13)	1(<1)	7(4)	-	
8-10	2(2)[a]	19(13)	11(5)	24(13)	-	
6- 8	7(6)	26(18)	25(13)	17(9)	-	
4- 6	15(13)	13(9)	25(13)	44(23)	3(3)	
2- 4	45(38)	28(20)	57(28)	50(27)	9(10)	
0- 2	48(41)	26(18)	83(41)	44(23)	80(87)	
Total	117(100)	144(100)	202(100)	188(100)	92(100)	
Stems/ha	509(15.7)[b]	626(19.4)	878(27.2)	817(25.3)	400(12.4)	3,230(100)

[a] % of Total

[b] % of Grand Total

the clumped dispersion of balsam poplar and aspen. The total density of trees was about two-thirds that in the lodgepole pine forest. Mean canopy height was 6.9 ± 2.1 m with a range of 0-12, slightly lower than the canopy height of the lodgepole pine forest. The average slope was $6.5 \pm 5.3°$ with a range of 0-20°.

The understory plants in the poplar and mixed forest included most of those found in the lodgepole pine forest type.

Relict Spruce Forest

Table 6 shows the number of cover values recorded for each species and the total vegetation in the overstory and middlestory of 17 random plots within the relict spruce forest. White spruce was present in all but one of the plots and was the dominant species, with three as the most common cover value. Other species were almost non-existant in the overstory.

Middlestory cover was very sparse with white spruce present in a third of the plots and willow present in about two-thirds of the plots. Other middlestory species were rarely present.

The DBH's and densities of trees in the 17 plots within the relict spruce forest are presented in Table 7.

The white spruce trees in the relict spruce forest were much larger than those of any species in the other forest types. Half of the white spruce trees had diameters greater

Table 6. Number of cover values for individual and combined species in the overstory and middlestory on 17 random plots within a relict spruce forest.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	1	-	-	-	-	-	-	-	-	-	1
4	3	-	-	-	-	-	-	-	-	-	4
3	8	-	-	-	-	-	-	-	-	-	7
2	4	1	-	1	-	-	-	-	-	-	5
1	-	-	1	-	4	-	-	-	-	-	-
0	1	16	16	16	16	-	13	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	5	-	-	-	-	-	6
1	5	-	1	2	6	-	-	3	1	3	9
0	12	17	16	15	6	17	17	14	16	14	2

* 6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1= present - 5%, 0= absent.

Table 7. Stem density by diameter class (DBH) of the overstory tree species in 17 random plots within the relict spruce forest community type.

Diameter class (cm)	Number of individuals in each diameter class					Grand Total
	Picea glauca	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix sp.*	
25-30	12(8)[a]	-	-	-	-	
20-25	12(8)	-	-	-	-	
18-20	8(6)	-	-	-	-	
16-18	4(3)	-	-	-	-	
14-16	-	-	-	-	-	
12-14	13(9)	-	-	-	-	
10-12	9(6)	-	-	-	-	
8-10	14(10)	-	-	-	-	
6- 8	12(8)	-	-	-	-	
4- 6	15(10)	1(50)	-	-	-	
2- 4	33(23)	1(50)	2(50)	2(100)	4(13)	
0- 2	13(9)	-	2(50)	-	26(87)	
Total	145(100)	2(100)	4(100)	2(100)	30(100)	
Stems/ha	1,706(79.3)[b]	24(1.1)	47(2.1)	24(1.1)	353(16.4)	2,154(100)

[a] % of Total

[b] % of Grand Total

than 8 cm and 25% were over 16 cm. Trees of other species in the relict spruce forest were small.

As in the consideration of canopy coverage and tree diameter, white spruce is the dominant tree, composing 79.3% of the total number of trees.

Mean canopy height was 13.9 ± 3.7 m with a range of 4-20 m. This is approximately twice as high as the average canopy height of the lodgepole pine and poplar and mixed forest types. The average slope of the plots was $3.8 \pm 2.9°$ with a range of 1-10°. Relict spruce forest was usually found in association with fairly level marshy areas.

The floor of the relict spruce forest was usually thickly covered with moss. Other common understory plants included rush (_Juncus_ _sp_.), horsetail (_Equisetum_ _sp_.), sedge (_Carex_ _sp_.), orchids (_Habenaria_ _sp_.), blueberry, twinflower, bunchberry and wintergreen.

Meadow and Marsh

Table 8 shows the number of cover values recorded for each species and the total vegetation in the middlestory of 22 random plots of meadow and marsh. No overstory vegetation occurred on the plots. The dominant species in the middlestory was willow, present in 64% of the plots. Other middlestory species were rare.

The average slope of the plots was 4.0 ± 3.1 with a range of 0-10.

Understory on the meadows was dominated by rough fescue

Table 8. Number of cover values for individual and combined species in the middlestory on 22 random plots within a meadow and marsh.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	1	-	-	-	-	-	1
3	-	-	-	-	4	-	1	-	-	-	6
2	1	-	-	2	7	1	2	-	-	-	7
1	1	-	-	-	2	-	-	-	-	-	1
0	20	22	22	20	8	21	19	22	22	22	7

* 6=>95-100%, 5=>75-95%, 4=>50-75%, 3=>25-50%, 2=>5-25%, 1= present - 5%, 0= absent.

(*Festuca scabrella*). The marshy areas were dominated by rushes and sedges.

RESULTS AND DISCUSSION

The results of this study have been organized under four major headings. The first section deals with the relationship of age of the bird to dispersion, the second with stage of reproductive cycle and dispersion, the third with habitats and dispersion and the fourth with dispersal.

Age and Dispersion

Age Determination

In order to determine the effect of age of the grouse on dispersion and dispersal it was desirable to divide the grouse into three age classes. The following scheme was used, with a bird hatched in July 1965 as an example:

Juvenile - July 1965 to April 30, 1966

Yearling - May 1, 1966 to April 30, 1967

Adult - May 1, 1967 -

At the beginning of this study no techniques for determining ages of Franklin's grouse were available. Petrides (1942) pointed out that the outer two primaries acquired with the juvenal plumage are retained by young grouse until their second summer and can be distinguished by their pointed tips from the corresponding remiges of adults, which have rounded extremities. On the basis of this criterion he reported that out of 82 Franklin's grouse study skins, five were of questionable age. He did not indicate whether the skins were of

known age. In this study, the criterion used by Petrides was found to be unreliable.

Van Rossem (1925) suggested that in spruce grouse the postjuvenal tail tended to differ from that of the adult but indicated that the material was not altogether satisfactory. P. W. Martin (in Lumsden and Weeden 1963: 589) noted that in Franklin's grouse, young of the year had little or no white on the tips of the upper tail coverts whereas adults had up to one-fourth inch of white on the tips of these feathers. He also indicated that more young birds than old birds have white tips on the central rectrices, that tails of adults are darker than those of young grouse, and that central tail feathers of adults are longer than the outer ones. Martin's observations must have been based on fall specimens since he indicated that ages were determined by moult pattern of the remiges.

In this study, the ability to determine the age of birds in the spring and early summer was of primary importance so that the age structure of the population being studied would be known. It is possible that over a period of several months white tips on feathers might wear and colors of feathers might fade (Welty, 1962: 45-46), complicating methods employing some of the characteristics suggested above. The need for objective criteria was therefore apparent. As a result, the first (proximal) primary, a central upper tail covert, and a central rectrix were plucked from captured birds and kept for measurements following a method W. Wishart (personal communication) was using for age determination in ring-necked

pheasants (Phasianus colchicus) with measurements of the first primary. Although tenth primaries were also plucked, no objective criteria could be discerned from these feathers that would distinguish yearlings from adults. Only mature feathers, i.e. feathers with a hard quill, were used. In a few birds, these feathers were plucked more than once. When this was done, care was taken not to use feathers which had replaced one previously. There was evidence that in some cases the replacing feathers developed abnormal characteristics. They often grew in smaller than normal and one primary grew in with a crooked shaft and white vane. The feathers were air dried for at least two months before measurements were made.

Measurements of feathers from female birds of known and estimated age are presented in Figures 2, 3, and 4. Birds of known age were those for which the age was known from banding records. Birds of estimated age were those for which the age was determined from an age classification scheme which will be presented below. It should be noted that the measurements of feathers taken from juveniles after post-juvenal moult were recording in the yearling age class. The measurements of feathers from yearlings after the first post-nuptial moult were recorded in the adult age class. In the case of each feather the distribution of measurements shows a definite clumping into yearling and adult age classes. This grouping is most striking for measurements of the first primary (Fig. 2). There was no overlap between yearling and adult age classes for the diameters of first primaries of

Figure 2. Measurements of first primary feathers of female Franklin's grouse in yearling and adult age classes. Measurements are plotted as diameter (to the nearest 0.1 mm of the rachis at the superior umbilicus) against length (to the nearest mm from the inferior umbilicus to the tip of the vane).

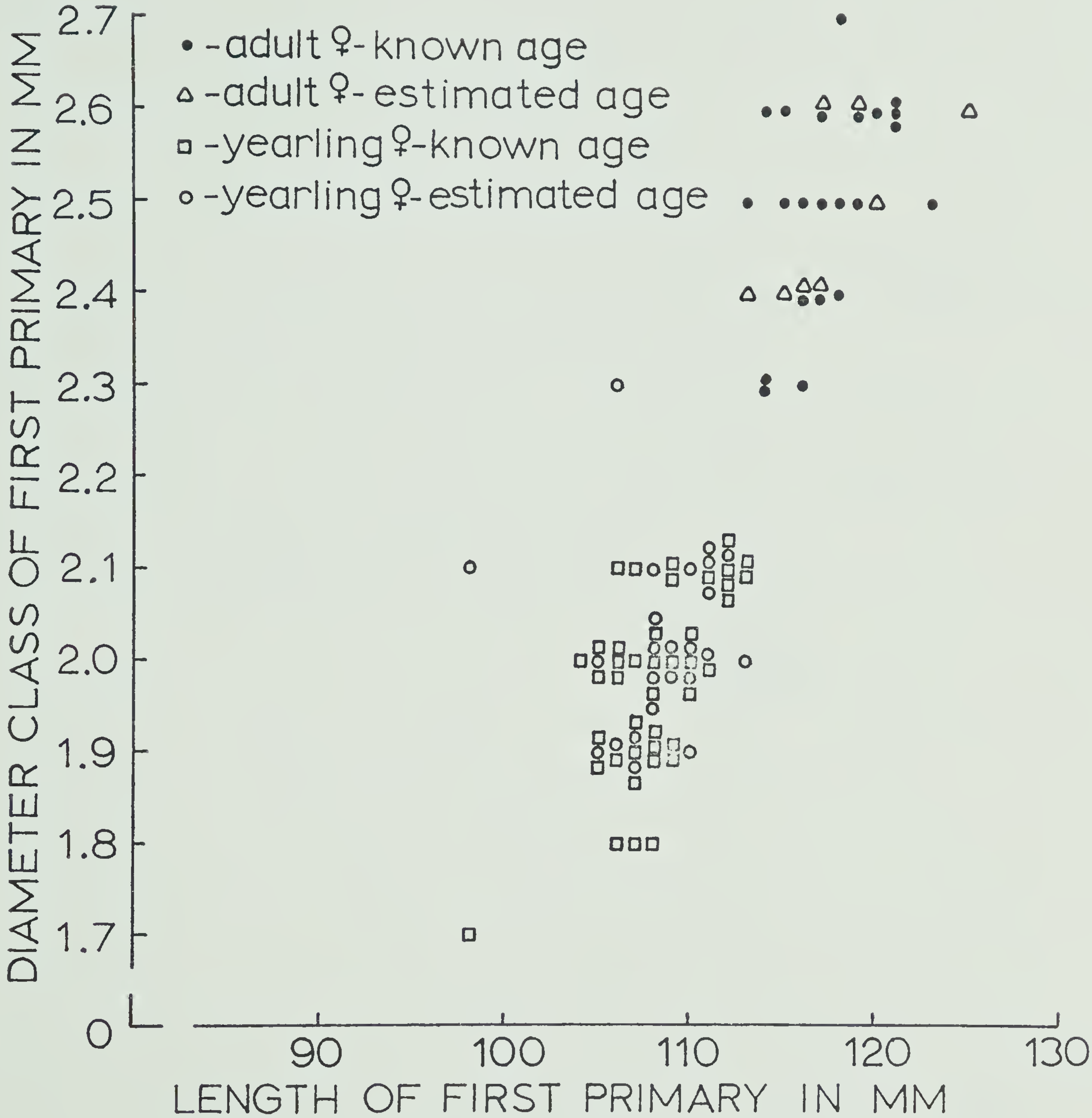

• -adult ♀- known age
△ -adult ♀- estimated age
□ -yearling ♀- known age
○ -yearling ♀- estimated age
DIAMETER CLASS OF FIRST PRIMARY IN MM
2.7
2.6
2.5
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
0
90
100
110
120
130
LENGTH OF FIRST PRIMARY IN MM

Figure 3. Measurements of central upper tail coverts of female Franklin's grouse in yearling and adult age classes. Measurements are plotted as diameter (to the nearest 0.1 mm of the rachis at the superior umbilicus) against length (to the nearest mm from the inferior umbilicus to the tip of the vane).

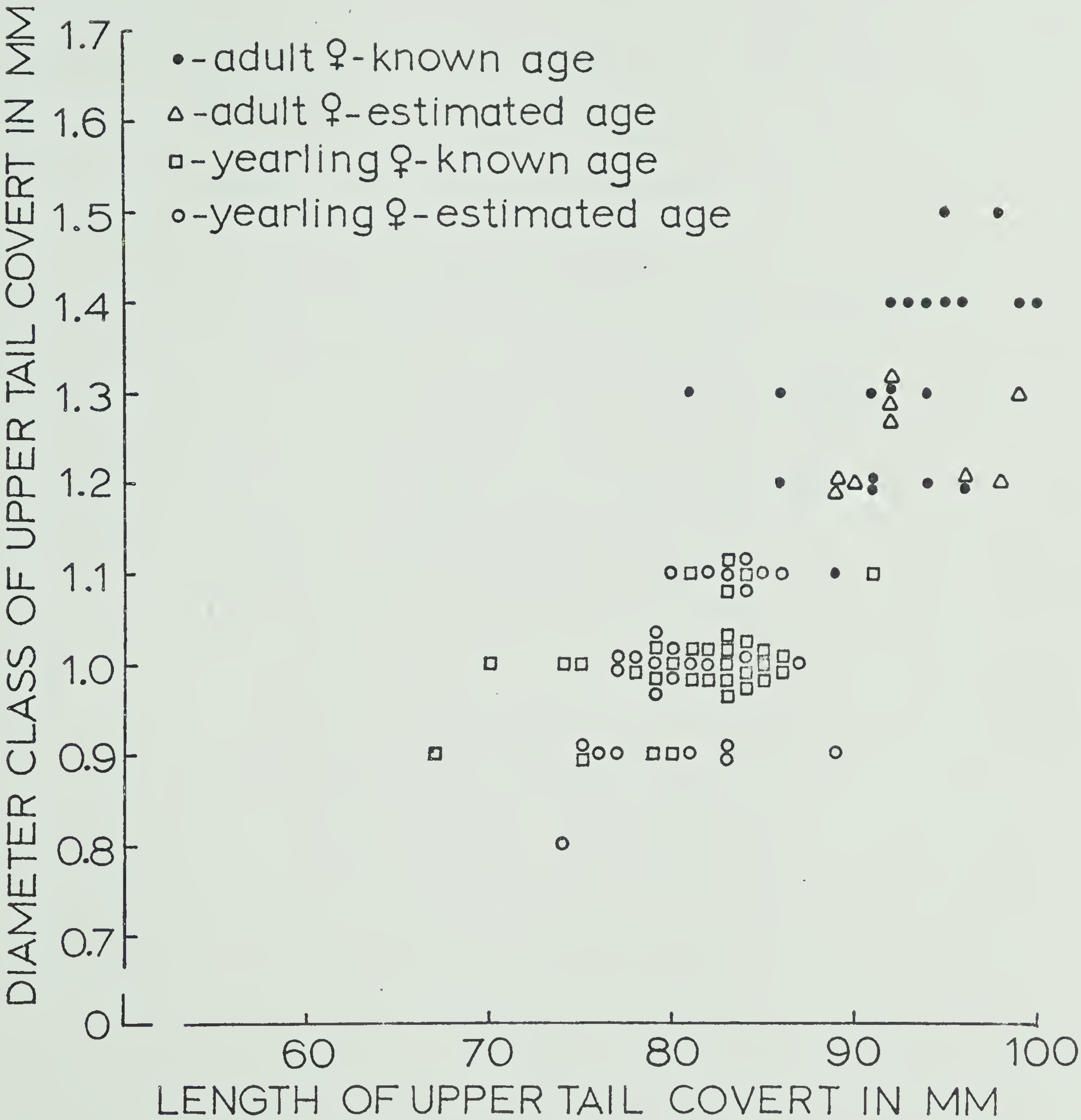

•-adult ♀-known age
△-adult ♀-estimated age
□-yearling ♀-known age
○-yearling ♀-estimated age
DIAMETER CLASS OF UPPER TAIL COVERT IN MM
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0
60
70
80
90
100
LENGTH OF UPPER TAIL COVERT IN MM

Figure 4. Measurements of central rectrices of female Franklin's grouse in yearling and adult age classes. Measurements are plotted as diameter (to the nearest 0.1 mm of the rachis at the superior umbilicus) against length (to the nearest mm from the inferior umbilicus to the tip of the vane).


•-adult♀- known age
▵-adult♀- estimated age
▫-yearling♀- known age
∘-yearling♀- estimated age
DIAMETER CLASS OF CENTRAL RECTRIX IN MM
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
0
90
100
110
120
130
LENGTH OF CENTRAL RECTRIX IN MM

birds of known age. Measurements of length of primaries of birds of known age shows two in the yearling age class and one in the adult age class in the region of overlap. Figure 3 shows a small degree of overlap between yearling and adult age classes for diameters of upper tail coverts of birds of known age. One adult female had an upper tail covert with a diameter of less than 1.2 mm. The overlap in lengths of upper tail coverts is more extensive than the overlap in lengths of primaries. Figure 4 shows that overlap in both lengths and diameter of central rectrices is greater than the overlap for the corresponding measurements of first primaries and upper tail coverts.

To facilitate evaluation of the measurements recorded in Figures 2, 3, and 4, the data for birds of known age as determined from banding records are summarized and treated statistically in Table 9. In the light of the varying degrees of overlap or lack of overlap in the measurements of the different feathers, it is valuable to know how reliable each measurement of each feather is when used alone to place birds into yearling and adult age classes. The reliability of using each of the six types of measurements can be calculated. It can be expressed as a percentage of cases each type of measurement could be used alone to place a bird in the correct age class. Solving for z in the following equation will give a value that can be compared with those appearing in a table of z values.

$$(s_A \times z) + (s_Y \times z) = \bar{x}_A - \bar{x}_Y$$

Table 9. Statistics of the measurements of diameter and length of the first primaries, central upper tail coverts, and central rectrices of female Franklin's grouse of known age in southwestern Alberta.

	Age	Sample Size (n)	Mean ($\bar{x}$)	Range	Standard Deviation (s)	$\bar{x} + 1.96s$
First Primary						
Diameter	A	22	2.50	2.3-2.7	.113	2.28- 2.72
	Y	41	1.98	1.7-2.1	.101	1.78- 2.18
Length	A	22	117.36	113-123	2.718	112.03- 122.69
	Y	41	107.98	98-113	2.880	102.34- 113.62
Central Upper Tail Covert						
Diameter	A	20	1.32	1.1-1.5	.111	1.10- 1.54
	Y	33	1.00	.9-1.1	.053	.90- 1.11
Length	A	20	92.65	81-100	4.64	83.56- 101.74
	Y	33	81.09	67- 91	4.80	71.69- 90.50
Central Rectrix						
Diameter	A	25	1.96	1.8-2.1	.086	1.80- 2.13
	Y	29	1.63	1.5-1.9	.088	1.45- 1.80
Length	A	25	118.04	109-128	4.34	109.53- 126.55
	Y	29	108.79	98-118	4.35	100.26- 117.32

A - Adult
Y - Yearling

s_A = standard deviation for the adult measurement

s_Y = standard deviation for the yearling measurement

$\bar{x}_A$ = mean for the adult measurement

$\bar{x}_Y$ = mean for the yearling measurement

z = value in table of z (Siegel, 1956)

The position of the z value gives a probability value that the two populations compared are similar. The reliability of

the method is the difference between the probability value and 100%. The reliability of using each of the measurements alone to place birds in the correct age classes were calculated to be the following: first primary diameter, 98.5%; first primary length, 90.7%; upper tail covert diameter, 94.8%; upper tail covert length, 78%; central rectrix diameter, 94.6%; central rectrix length, 71%.

In the case of the measurements of the primary, the diameter alone differentiated yearlings of known age from adults of known age with 100% accuracy. However, when the variation within the data is taken into account as it is in the calculation of the reliability figure, one can expect that in future cases, the primary diameter could be used to differentiate yearlings from adults in about 99% of the cases. Each of the other five types of measurements are less reliable, but of these, the diameter measurements are the best.

Using the distribution of measurements in the column headed " $\bar{x} \pm 1.96s$ " of Table 9, a scheme has been developed for placing birds in age classes when any or all of the six possible measurements of feathers are available. (The mean plus or minus 1.96 standard deviations should include 95% of the population.) This scheme is presented in Table 10. Specific values were assigned arbitrarily to individual feathers such that those falling into the adult range were given a value of +1.0, and those into the yearling range, a -1.0 except for the first primary diameter. Since the diameter of the first primary when used alone has a reliability

Table 10. Scheme for determining the age of female Franklin's grouse in southwestern Alberta based on measurement of diameters and lengths of the first primary, central upper tail covert, and central rectrix of of females of known age.

	Measurement	Age	Value
First Primary			
Diameter	≥ 2.3	A	+1.5
	≤ 2.2	Y	-1.5
Length	≥ 115	A	+1.0
	≤ 111	Y	-1.0
Central Upper Tail Covert			
Diameter	≥ 1.2	A	+1.0
	≤ 1.0	Y	-1.0
Length	≥ 92	A	+1.0
	≤ 83	Y	-1.0
Central Rectrix			
Diameter	≥ 1.9	A	+1.0
	≤ 1.7	Y	-1.0
Length	≥ 118	A	+1.0
	≤ 109	Y	-1.0

A - Adult
Y - Yearling

of more than 95% it should be given more weight. Therefore, it was assigned a value of +1.5 if on the adult side and -1.5 if on the yearling side. If the values when totalled give a positive sum the bird is an adult. If the sum is negative, the bird is a yearling. If the sum is zero, the bird is of questionable age. Examples in Table 11 illustrate this scheme.

Using the technique described above, when measurements of all these feathers were available, all of 37 birds of known

Table 11. Examples of determination of age class of female Franklin's grouse from which some or all of the measurements of diameter and length of the first primary, a central upper tail covert, and a central rectrix are known.

	Primary				Tail Covert				Rectrix				Total	Age
Bird No.	D	V	L	V	D	V	L	V	D	V	L	V		
187 B1	2.6	+1.5	114	0	1.5	+1.0	95	+1.0	2.0	+1.0	115	0	+4.5	A
173 B1	1.9	-1.5	109	-1.0	1.0	-1.0	81	-1.0	1.6	-1.0	106	-1.0	-6.5	Y
513 Y	2.5	+1.5	113	0	1.2	+1.0	86	0	1.9	+1.0	109	-1.0	+2.5	A
B22923 A1	-	-	-	-	1.4	+1.0	99	+1.0	2.0	+1.0	118	+1.0	+4.0	A
B16848 A1	-	-	-	-	-	-	-	-	1.9	+1.0	118	+1.0	+2.0	A
132 B1	2.3	+1.5	106	-1.0	1.0	-1.0	79	-1.0	1.4	-1.0	97	-1.0	-3.5	Y

D - diameter in mm
L - length in mm
V - arbitrary values assigned as +1.0 to measurements of feathers of adult size, -1.0 to those of yearling size, and 0 to those which were not definitely (95% confidence) either adult or yearling size. Because of the high reliability (98.5%) of primary diameter measurements for separating adults from yearlings, they were assigned values of ± 1.5.

age were placed in the correct age class. When measurements of two or more feathers were available, all of 56 birds of known age were placed in the correct age class. When measurements of one or more feathers were available, 76 out of 77 birds of known age were placedin the correct age class.

The scheme was also used to determine the ages of birds of which the exact age was not known but from which the feather measurements were available. When measurements of the three feathers considered were known, 30 out of 30 birds could be placed into specific age classes. In one case (bird number 132 Bl in the examples in Table 11) the measurement of the primary diameter indicated that the bird was an adult. The other measurements, however, all fell into the yearling categories and consequently received negative values. The result was a total of -3.5 indicating that the bird was probably a yearling. The age classes of 56 out of 58 different birds, whose exact age was not known, were determined by this method and the measurements for the feathers are plotted in Figure 2, 3, and 4. For one of the two birds which could not be placed in an age class, measurements of only the rectrix and tail covert were known. For the other, measurements of only the rectrix were known. Only values of zero could be assigned to any of these measurements for the feathers of either of these birds.

When measurements of the three feathers are known, the technique described is almost 100% reliable. The reliability decreases as fewer of the measurements are available. However,

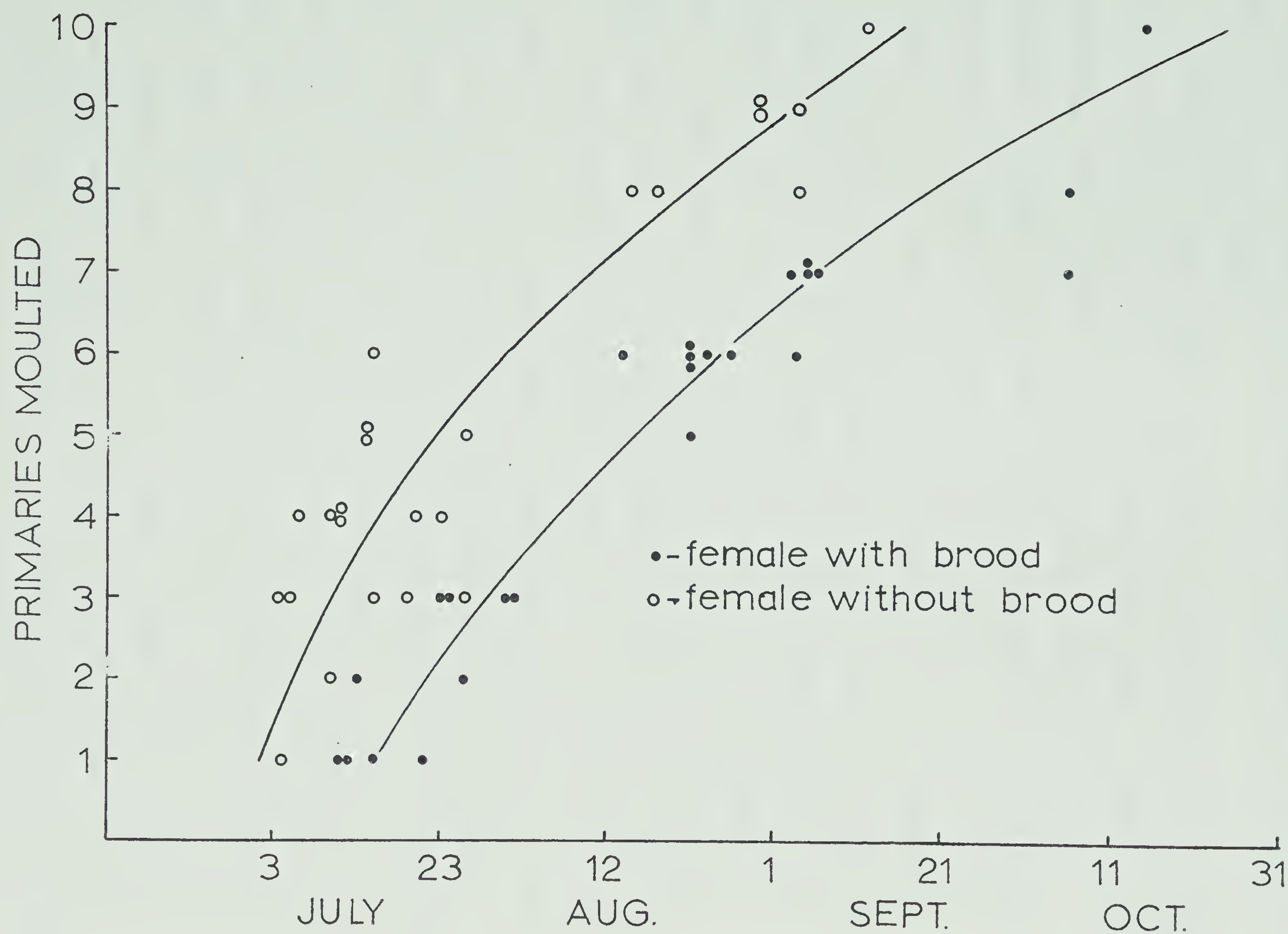
as long as there is a measurement of the diameter of the first primary, the reliability is not likely to decrease to less than 99%.

The period of time in which birds can be separated into age classes on the basis of feather measurements is governed by the timing of the moult. Stoneberg (1967) reported that in Montana adult and yearling female Franklin's grouse began to moult about the second week in June. The timing of primary loss in the two reproductive classes of females considered in this study is shown in Figure 5. Because of the small amount of data for any one year, data for the four years of the study have been combined. It appears that females without broods commenced moult of their primaries by about the fourth week in June. The beginning of the moult in females with broods was delayed approximately two weeks i.e. until about the second week in July.

Moulting of the rectrices began about when the third primary was moulted. This was the second week of July for females without broods and the fourth week of July for females with broods. Moult of the upper tail coverts occurred about the same time.

The onset of the moult thus limits the time during which yearlings may be distinguished from adults to about 8 to 11 weeks counting from May 1 in females without broods, and 10 to 13 weeks in females which have broods. However, the technique may be used from September to the following May to distinguish juveniles from adults and yearlings. During this

Figure 5. Sequence and timing of primary loss during the moult in female Franklin's grouse with and without broods.


PRIMARIES MOULTED
10
9
8
7
6
5
4
3
2
1
•-female with brood
o-female without brood
3
23
12
1
21
11
31
JULY
AUG.
SEPT.
OCT.

time feather measurements of the juveniles are in the yearling class and those of both yearlings and adults fall into the adult size class.

During the time this study was in progress, three people have presented techniques for determining age of spruce grouse. Stoneberg (1967) used a combination of criteria to age Franklin's grouse. He found that a comparison of the shape and color of the eighth and ninth primaries was not always reliable. He noted that the color of the central rectrix was also useful for age determination but suggested that the difference between age classes of females was subtle. He indicated that the length of the central rectrix could be used to determine age. However, the results of this study have shown that this criterion has a reliability of only 71%.

A technique for determining the age of Franklin's grouse by tails alone was presented by Zwickel and Martinsen (1967). The criteria for classifying age consisted of differences in coloration of the central rectrix along with the amount of white on the tips of the upper tail coverts. A test in which biologists placed 23 female tails into the correct age classes resulted in 100% accuracy. The birds from which tails were taken were shot in September and October. At this time the tail feathers would be no more than a couple of months old. The present study indicated that the tail feathers of birds in May and June showed evidence of fading and wear at the tips when compared with fresh feathers taken from birds in the fall. For these reasons the technique may not be reliable after a time lapse of several months.

Ellison (1968a) described a method to determine the age of Alaskan spruce grouse (Canachites canadensis osgoodi) based on the appearance of the ninth and tenth primaries. As has already been indicated, this subjective criterion was found unreliable for determining the age of Franklin's grouse in this study. Stoneberg (1967) also found this method unreliable for determining the age of Franklin's grouse in Montana.

Age Structure and Numbers

Before examining the effect of age of female Franklin's grouse on their dispersion, a knowledge of the numbers in each age class involved is important. The age structure of the female portion of the population of grouse on the main study area is presented in Table 12.

Table 12. Age structure of the female portion of a population of Franklin's grouse in southwestern Alberta during the period 1965-1968.

	Newly Banded			Previously Banded		Total				% Yearling
	A	Y	U	A	Y	A	Y	U	Total	
1965	3	2	8			3	2	8	13	40
1966	10	3	5	9	2	19	5	5	29	21
1967		7	4	16	3	16	10	4	30	38
1968	1	15		16		17	15		32	47

A - Adult
Y - Yearling
U - Female of unknown age

In Table 12, the percentage of yearlings present in the population has been computed for each year. Birds of unknown age were not considered in the calculations. Chi-square tests indicated that the difference in the ratio of yearlings to adults between years is not statistically significant. Combining the data for the four years shows that 32 out of 87 or 37% of the birds were yearlings.

The total number of adult and yearling females present on the main study area each year with the exception of 1965 is shown in Table 12. Since only part of the study area was used in 1965 and less time was spent on it than in the other years of the study, the number of grouse banded is lower than for other years. The numbers presented in the table represent the numbers of birds banded on the study area. Confidence in these numbers as a fairly accurate representation of the numbers of yearlings and adults actually on the study area during the period of study each year is based on the following facts. Every unbanded grouse seen on the main and auxiliary study area was captured and banded. In addition, the population of females was estimated using a method used by Boag (1958) to estimate populations of blue grouse. Boag used a formula given by Lagler (1949) for estimating fish populations and which was based on the ratio of marked to unmarked fish recaptured after a sample had initially been marked and released. In application to blue grouse Boag presented the formula as follows:

$$P = \frac{AB}{C}$$

Where P = the estimated population on any date

A = numbers of grouse seen on any date

B = number of marked grouse present on the study area on any date

C = number of marked grouse seen on any date

For any estimate (P), the numbers substituted for A, B, and C must represent data for which the date is the same.

Appendices 1, 2, 3, and 4 show the application of the formula and the estimated population of adult and yearling females on the study area for the years 1965, 1966, 1967, and 1968. As the numbers of observations increased, the more stable the population estimate became until it followed very closely the actual number banded. The estimate of the number of females arrived at for the population in 1965, 1966, 1967 and 1968 are 11, 28, 30, and 33 respectively. These estimates compare with 13, 29, 30, and 32 respectively as the numbers banded. By extrapolation using the proportion of the study area covered in 1965 the population of females on the main study area in 1965 was estimated to be 26. The population of adults and yearlings appeared to be fairly stable in 1966, 1967, and 1968 indicating that some factors or factor may be operating to keep the population at this level.

A third feature of Table 12 is that it shows that virtually all new recruits coming into the population are yearlings. In 1967 and 1968, only one new bird banded was determined to be an adult. Only a small portion of the home range of this bird was within the boundaries of the study

area, thus it was likely present but not intercepted the previous year.

Some Relationships Between Age and Dispersion

Since yearling birds are the new recruits entering the population, one might expect differences between their pattern of dispersion and the pattern of dispersion of adults. The influence of the age of a bird on two aspects of dispersion was examined. The home range size and the longest dimension of the home range were compared in yearling and adult birds to determine whether there was a difference in actual mobility between these age classes.

The sizes of home ranges were determined by plotting on an aerial photograph of the study area the points of observation of a bird in any one year. The outside points were joined and the area enclosed in the resulting polygon was determined. Home ranges of all birds with a minimum of four observations during a year were considered. A total of 23 home ranges of 10 different adults and 9 different yearlings were plotted.

Before comparing the sizes and longest dimensions of home ranges of adults and yearlings, it is advisable to determine the effect of the number of observations of a bird upon the size and longest dimension of its home range. Successive home ranges were plotted for each bird using the observations of the bird in chronological order. The area and longest dimension of the home range were determined after each additional observation was plotted. The resulting data

are presented in Figures 6 and 7. Figure 6 shows the mean percentage of the total size of the home range plotted against the number of observations. Figure 7 shows the mean percentage of the total longest dimension plotted against the number of observations. The area and longest dimension of the home range increase with the number of observations. The lack of data on birds which have been observed many times precludes an estimate of the number of observations needed to be confident that the home range size will not increase significantly with additional observations.

A comparison of the estimated size of home ranges of adult and yearling females is presented in Table 13.

A t-test was done to compare the mean size of the home range of adults and yearlings. The sizes were not statistically significantly different. Since the means for the size of home range show a tendency of the yearling females to wander more than adults, the small value of t may well be a result of a combination of small sample size and a high degree of variation in the size of home ranges. The relationship between number of observations and size of home range indicated in Figure 6 lends support to the tendency for yearlings to utilize a larger area than adults since the mean number of observations on which home range size was based was smaller for yearlings than for adults.

The longest dimension of the home ranges of adult and yearling females is shown in Table 14.

A t-test comparing the mean longest dimension of the

Figure 6. Relationship between area of home range and numbers of observations of female Franklin's grouse in southwestern Alberta.

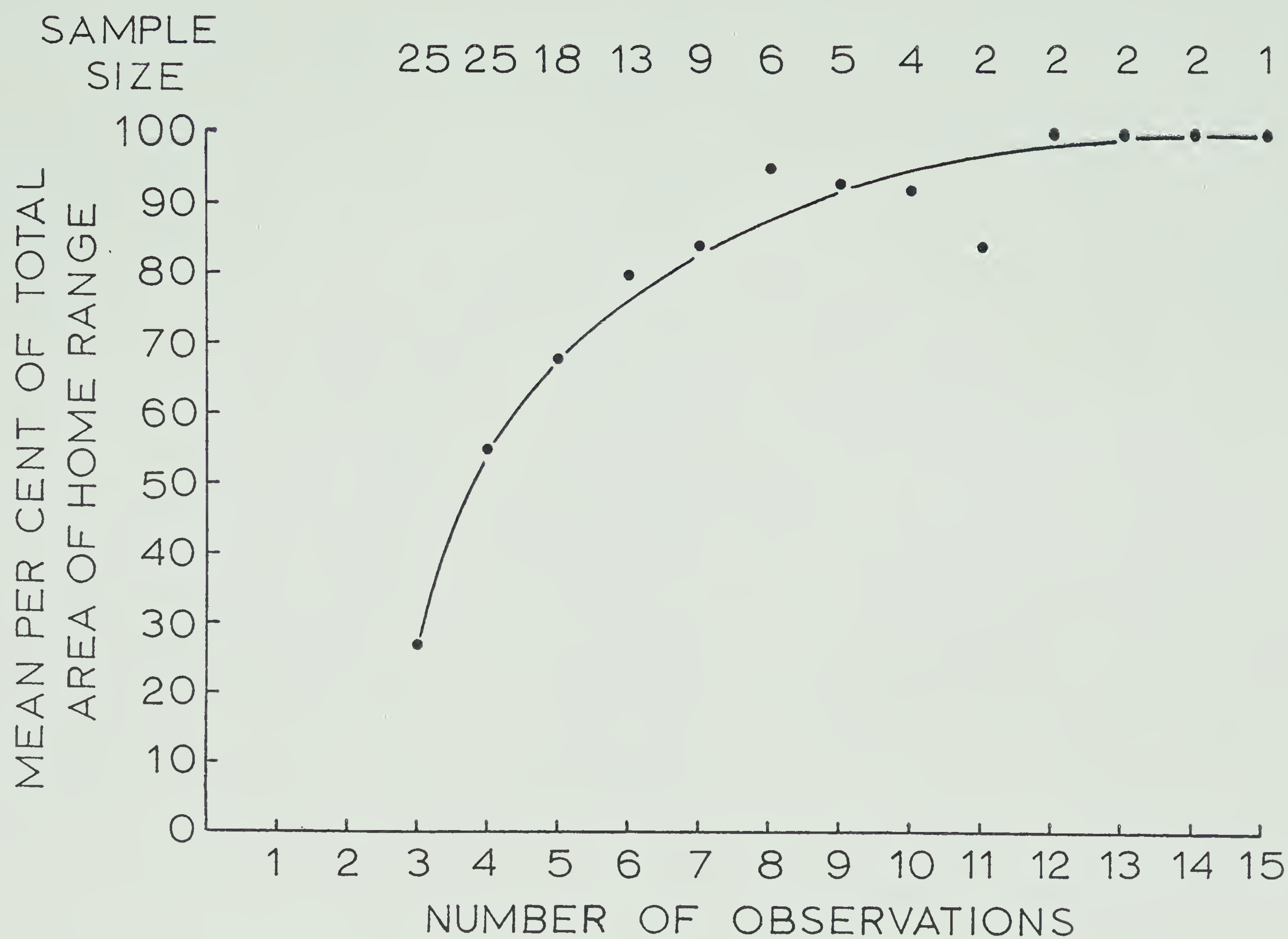

SAMPLE SIZE
25 25 18 13 9 6 5 4 2 2 2 2 1
MEAN PER CENT OF TOTAL AREA OF HOME RANGE
100
90
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
NUMBER OF OBSERVATIONS

Figure 7. Relationship between longest dimension of home range and numbers of observations of female Franklin's grouse in southwestern Alberta.

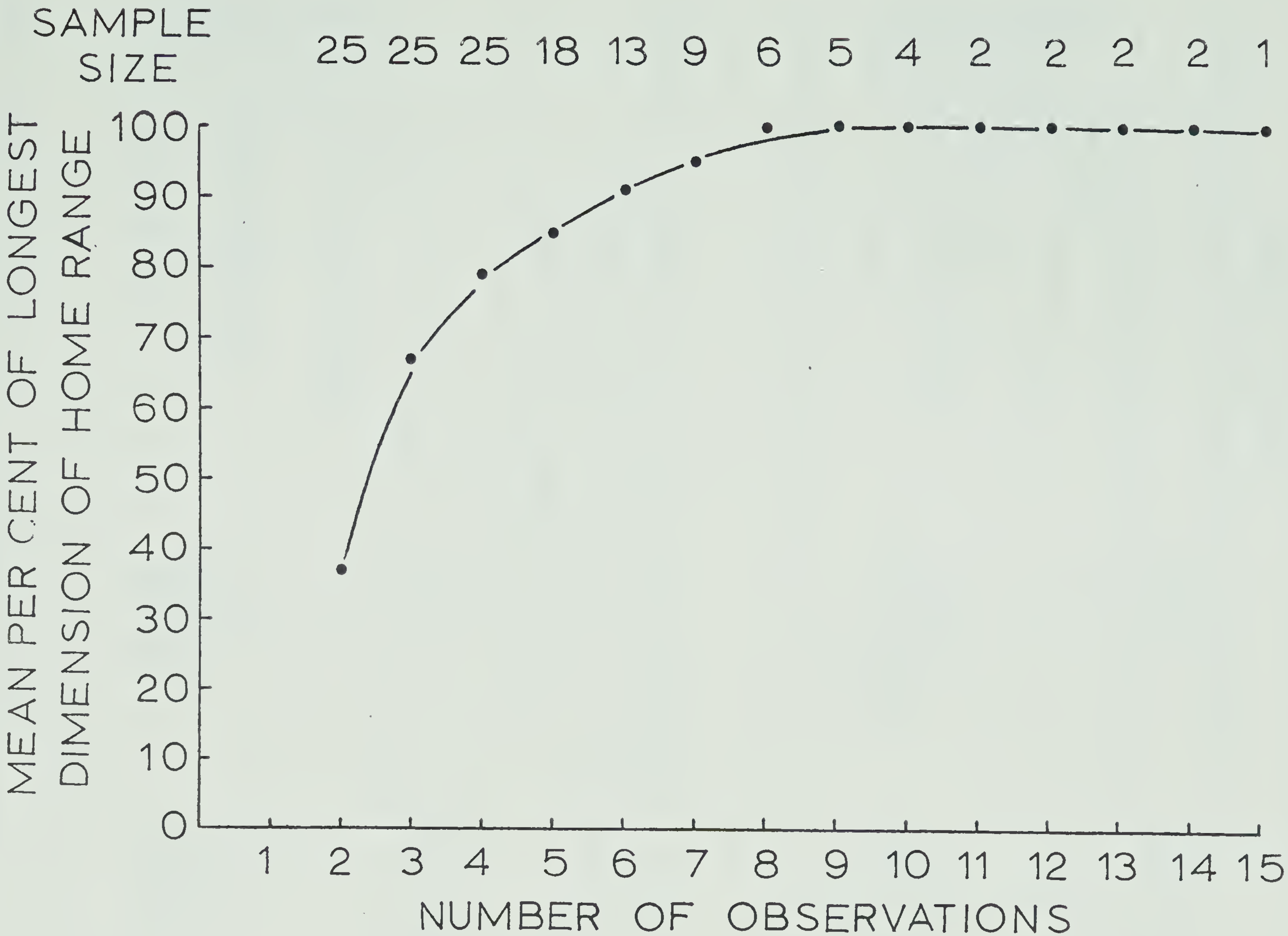

SAMPLE
SIZE
25 25 25 18 13 9 6 5 4 2 2 2 2 1
MEAN PER CENT OF LONGEST
DIMENSION OF HOME RANGE
100
90
80
70
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
NUMBER OF OBSERVATIONS

Table 13. Comparison of the size of the home range of adult and yearling female Franklin's grouse in southwestern Alberta.

	Adult	Yearling
No. of birds	14	9
Mean no. of observations per bird	8	5
Range in no. of observations per bird	4-15	4-8
Mean size of home range	5.87 ha	13.36 ha
Range	.50-17.81 ha	1.74-45.75 ha
Standard Deviation	5.71 ha	14.04 ha

Table 14. Comparison of the longest dimension of the home ranges of adult and yearling female Franklin's grouse in southwestern Alberta.

	Adult	Yearling
No. of birds	14	9
Mean no. of observations per bird	8	5
Range in no. of observations per bird	4-15	4-8
Mean longest dimension	463 m	817 m
Range	130-1,232 m	475-1,344 m
Standard Deviation	287 m	289 m

home ranges of adults and yearlings showed a significant difference. Yearling females tend to wander more than adults. Because of this, age of the birds will always be taken into consideration when the influence of the stage of reproductive

cycle and habitat upon dispersion is considered in the sections to follow.

Stage of Reproductive Cycle and Dispersion

Age Determination of Juveniles

The moult of primaries in several species of juvenile galliforms has been used as an indicator of age and, incidentally, to date stages of the reproductive cycle of breeding females. Age determination techniques for juveniles based on primary moult have been developed for ring-necked pheasants (*Phasianus colchicus*), bobwhite quail (*Colinus virginianus*), and Hungarian partridge (*Perdix perdix*) by Thompson and Taber (1948); for ruffed grouse by Bump *et al.* (1947); and for blue grouse by Smith and Buss (1963) and Zwickel and Lance (1966). Consequently, it seemed feasible to attempt to do this with Franklin's grouse as well.

Chicks were individually marked and primary feathers measured. The sex of chicks could be assessed at five to six weeks of age by a method used by Ellison (personal communication) for Alaskan spruce grouse. At this time the postjuvenal feathers of the ventral pterylae appear. The breast feathers of males are black with white tips while those of females are white tipped and have white or buffy brown bars on a black background.

The data gathered were used to construct growth curves for groups of primaries. The growth curves, which can be used to estimate the age of chicks from hatching until approximately

ten weeks of age, are presented in Figures 8 and 9. The construction of the growth curves is based on measurements of primaries of chicks from three different broods of known age, plus data in which the time interval between measurements of the primaries of chicks of unknown age was known.

Curve A in Figure 8, in which the total length of juvenal primaries 6 through 10 are plotted, is the basis for the rest of the curves, which are presented. It was constructed in the following way. First, data from birds of known age were plotted. These included 18 sets of primary measurements from 12 different birds, at four different ages up to 19 days. The best line drawn through these plotted points was used to determine the age of all the other chicks from which primary measurements had been taken by the time they were 19 days of age. These latter data were used to complete the construction of curve A and were also used to construct curve B in Figure 8 and the curves presented in Figure 9. The validity of using the curve based on measurements of chicks of known age up to 19 days of age, to estimate the ages of all other chicks from which primaries had been measured by the time they were 19 days old, is supported by the fact that, up to this date at least, there is no evidence of sex-related difference in growth rate of juvenal primaries. Furthermore, none of the measurements up to 19 days of age were displaced from the curve by more than one day. There appears to be little or no difference in growth rate of juvenal feathers between the sexes nor in the absolute lengths

Figure 8. Growth of juvenal primaries of juvenile Franklin's grouse in southwestern Alberta. Curve A shows the growth of juvenal primaries 6-10 and is plotted as the summed length of these five primaries in mm versus the age in days. In addition to the measurements of primaries from birds of known age, the curve is composed of known-interval data including 19 measurements of nine different juvenile males, 21 measurements of nine different juvenile females, and 14 measurements of six different juveniles of unknown sex. Curve B shows the growth of juvenal primaries 9 and 10, and is plotted as the total length of these primaries in mm versus the age in days. The curve is composed of 4 measurements of the primaries of four different juveniles of known-age, 45 measurements of nine different juvenile males, and 38 measurements of nine different juvenile females.

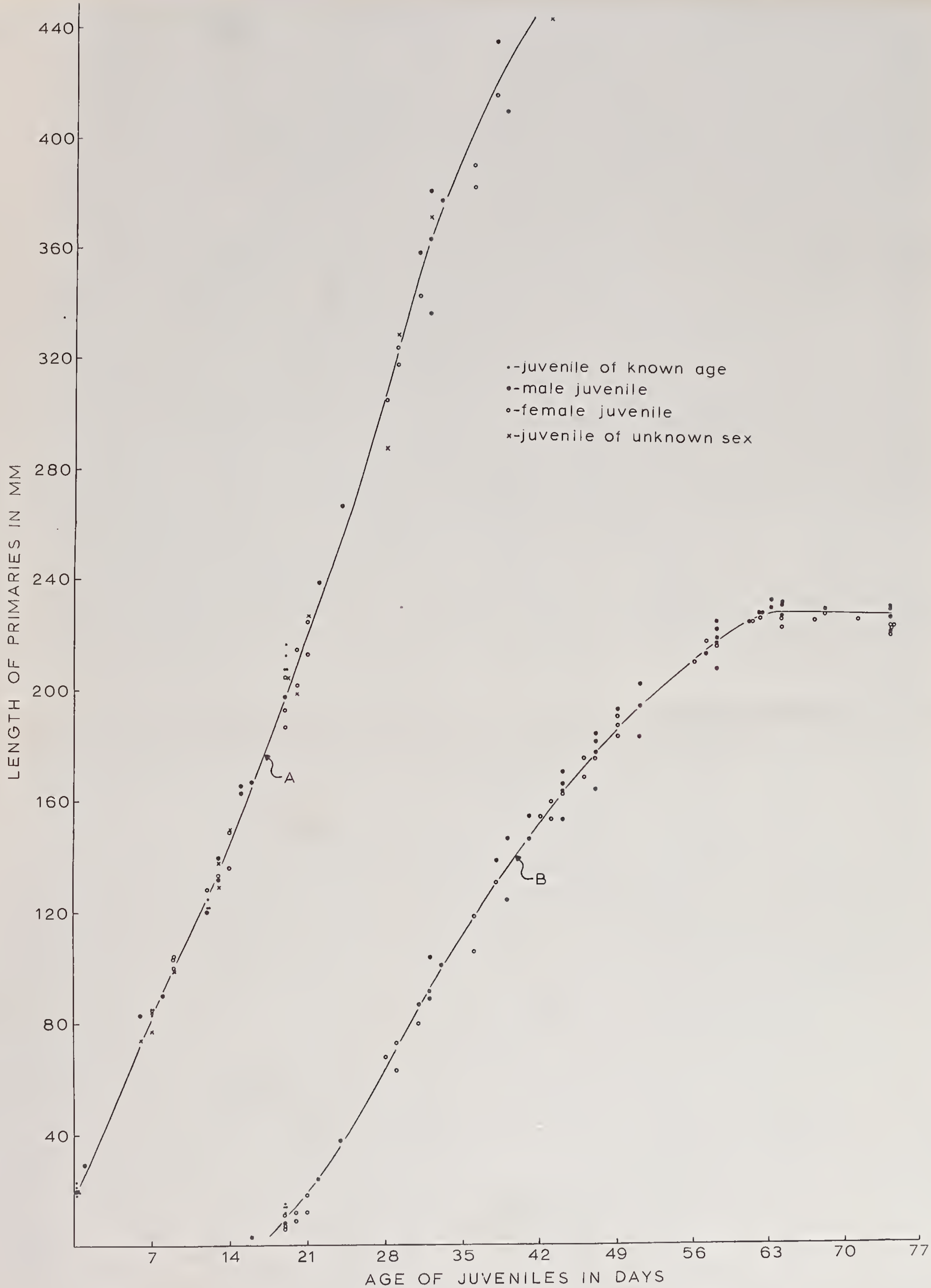
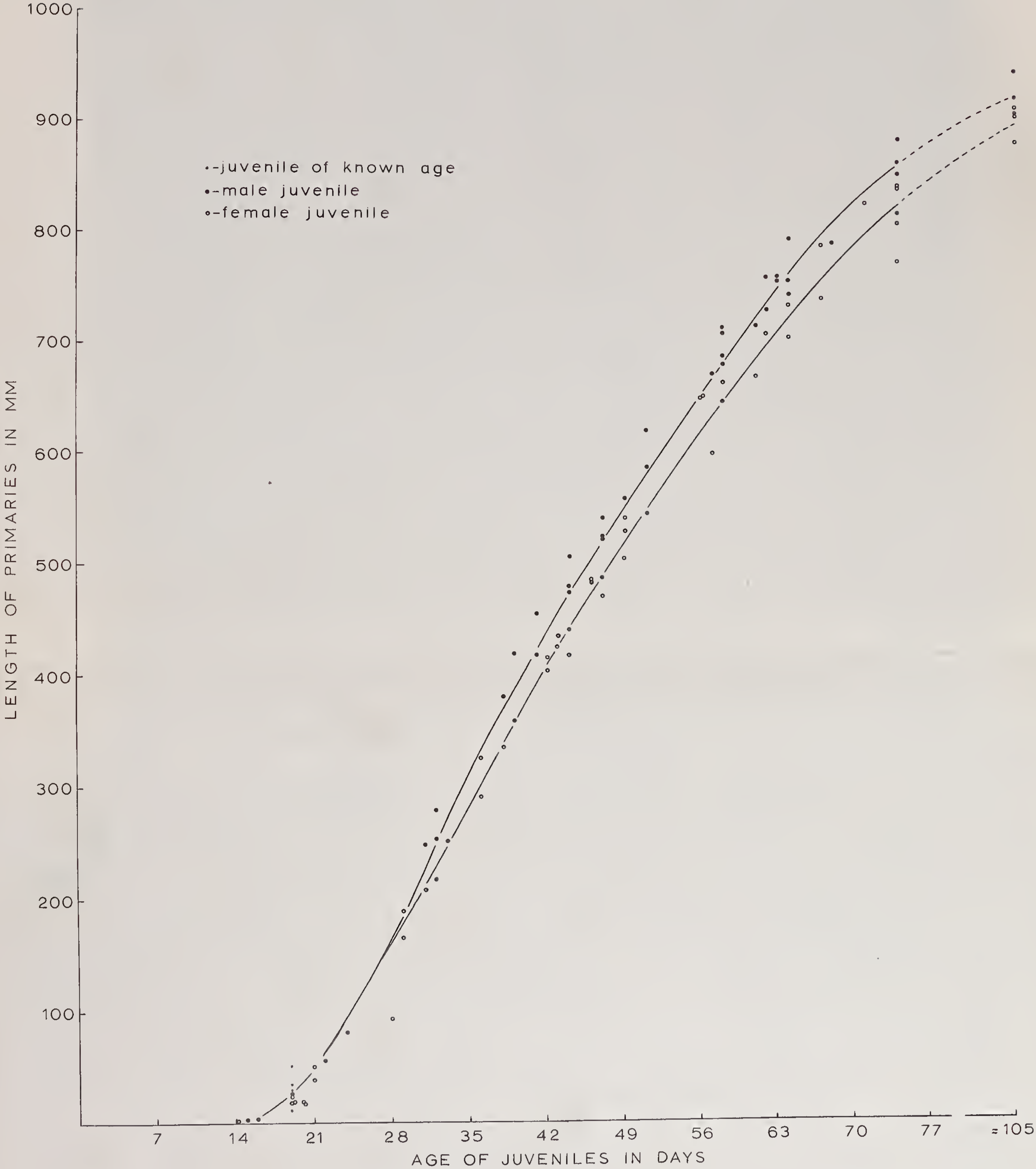

LENGTH OF PRIMARIES IN MM
440
400
360
320
280
240
200
160
120
80
40
7
14
21
28
35
42
49
56
63
70
77
AGE OF JUVENILES IN DAYS
A
B
•-juvenile of known age
•-male juvenile
∘-female juvenile
×-juvenile of unknown sex

Figure 9. Growth of postjuvenal primaries of juvenile Franklin's grouse in southwestern Alberta. The curves presented show the growth of the postjuvenal primaries and are plotted as the total length of the postjuvenal primaries which are present versus the age in days. The curves are composed of 4 measurements of four different juveniles of known-age, 46 measurements of nine different juvenile males, and 41 measurements of nine different juvenile females in addition to the measurements of birds taken in October.


•-juvenile of known age
•-male juvenile
∘-female juvenile
LENGTH OF PRIMARIES IN MM
1000
900
800
700
600
500
400
300
200
100
7
14
21
28
35
42
49
56
63
70
77
≈105
AGE OF JUVENILES IN DAYS

achieved. The points plotted for the sum of the measurements of juvenal primaries numbers nine and ten (curve B, Figure 8) show that there is little or no difference in growth rate between males and females until these feathers are maturing at approximately nine weeks.

It appears that measurements of the juvenal primary remiges can be used to estimate the ages of most juvenile Franklin's grouse to within two days up to the age of eight weeks. Of 66 points plotted in curve A up to 35 days, 63 or 95% of them are within one day of the line drawn through the points. In curve B, up to 8 weeks, 53 out of 55 or 96% of the points fell within 2 days of the line. After 8 weeks, the rate of growth of the two distal juvenal primaries decreases. This results in a small difference in total length of the primaries representing a relatively large difference in time. Therefore, measurements of these primaries are only useful up to 8 weeks of age even though they may not be fully grown for another ten days.

A difference in the growth curves of postjuvenal primaries of males and females is shown in Figure 9. The main reason for this difference is that the primaries of males usually grow to a greater absolute length than in females. Out of 58 points representing lengths of postjuvenal feathers plotted up to 8 weeks, 55 or 95% of them fell within 2 days of the curves. All but one of the points were within three days of the lines. The advantage of the growth curve for the postjuvenal primaries lies in the fact that they can be used

to determine the age of chicks after the time when juvenal curves are no longer useful. The data plotted in Figure 9 up to 74 days shows that 98% of 91 points fell within 3 days of the line.

In Figure 9, hypothetical curves have been drawn to complete the postjuvenal primary growth curves of male and female juveniles. This was done by extrapolation of the curves which had been plotted up to 74 days to points which represent average measurements of mature sets of postjuvenal primaries. The measurements which the averages represent were taken from birds captured in the second and third weeks of October. Measurements from four birds from three different broods during the first week of October indicated that postjuvenal primary growth was not complete at this time. The time span of the hypothetical curve is approximately four weeks. Theoretically, then, one may be able to roughly estimate the age of juveniles during the period from approximately 10 to 14 weeks of age on the basis of the hypothetical curve. However, during this time the growth rate of the postjuvenal primaries is decreasing rapidly resulting in a small difference in total length for a relatively large difference in time. This problem could possibly be rectified by examining the lengths of the seventh or eighth primaries individually, but at this time variation in the length of individual feathers of different birds of the same age is large. Therefore, it is probably not feasible to attempt to accurately estimate the age of juveniles on the basis of

measurements of primary remiges after the chicks are approximately 11 weeks of age.

The technique described above for determining the age of juvenile Franklin's grouse differs in one major respect from the methods described for age determination of other juvenile galliforms. This technique is based mainly on development of the juvenal primaries whereas, most others are based on postjuvenal primaries.

Weights of juvenile male and female Franklin's grouse were plotted against time to determine their value as an indicator of age (Figures 10 and 11). Weights from birds of known age are included along with those from which the age was determined from the primary growth curves. There appeared to be very little difference in the size of the male and female juveniles up to approximately eight weeks of age. After this time, weights of the males surpass those of the females. Up to the age of 10 weeks, 90% of 161 weights of juvenile males and females fell within five days of the best line drawn through the points. Therefore, weights may be used as a rough indicator of age but are certainly inferior to growth of primaries in this respect.

Chronology of Reproductive Events

To describe patterns of dispersion over the summer, it is necessary to determine as accurately as possible the periods of the year during which various factors related to the reproductive cycle may have their effects on dispersion.

Figure 10. Growth curves for body-weight of juvenile male Franklin's grouse in southwestern Alberta. The mean weights of 12 birds of known age but unknown sex are plotted on the graph. These mean weights were for all birds captured on a particular day. In addition, the graph includes 83 weights of 43 birds.

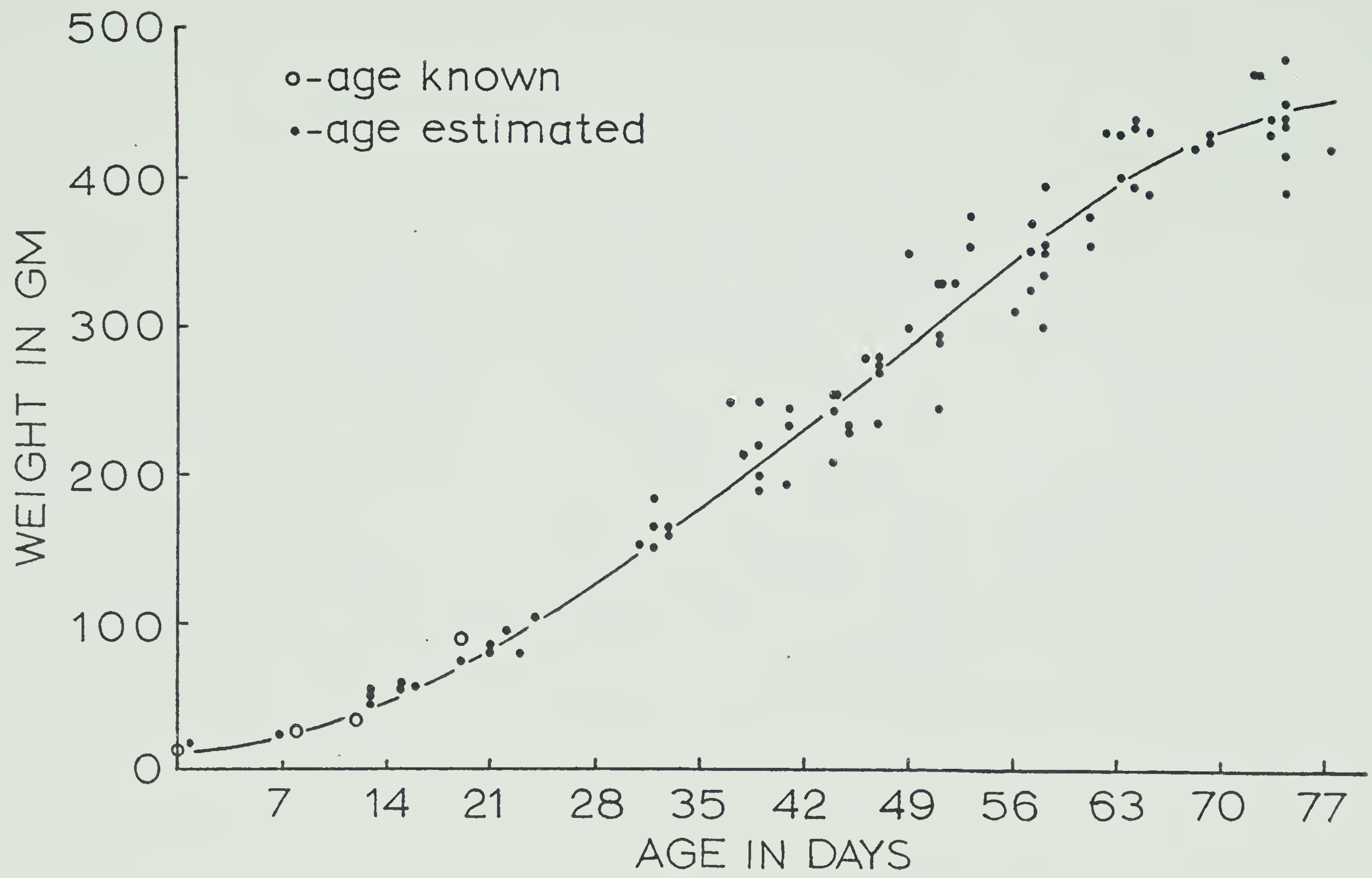
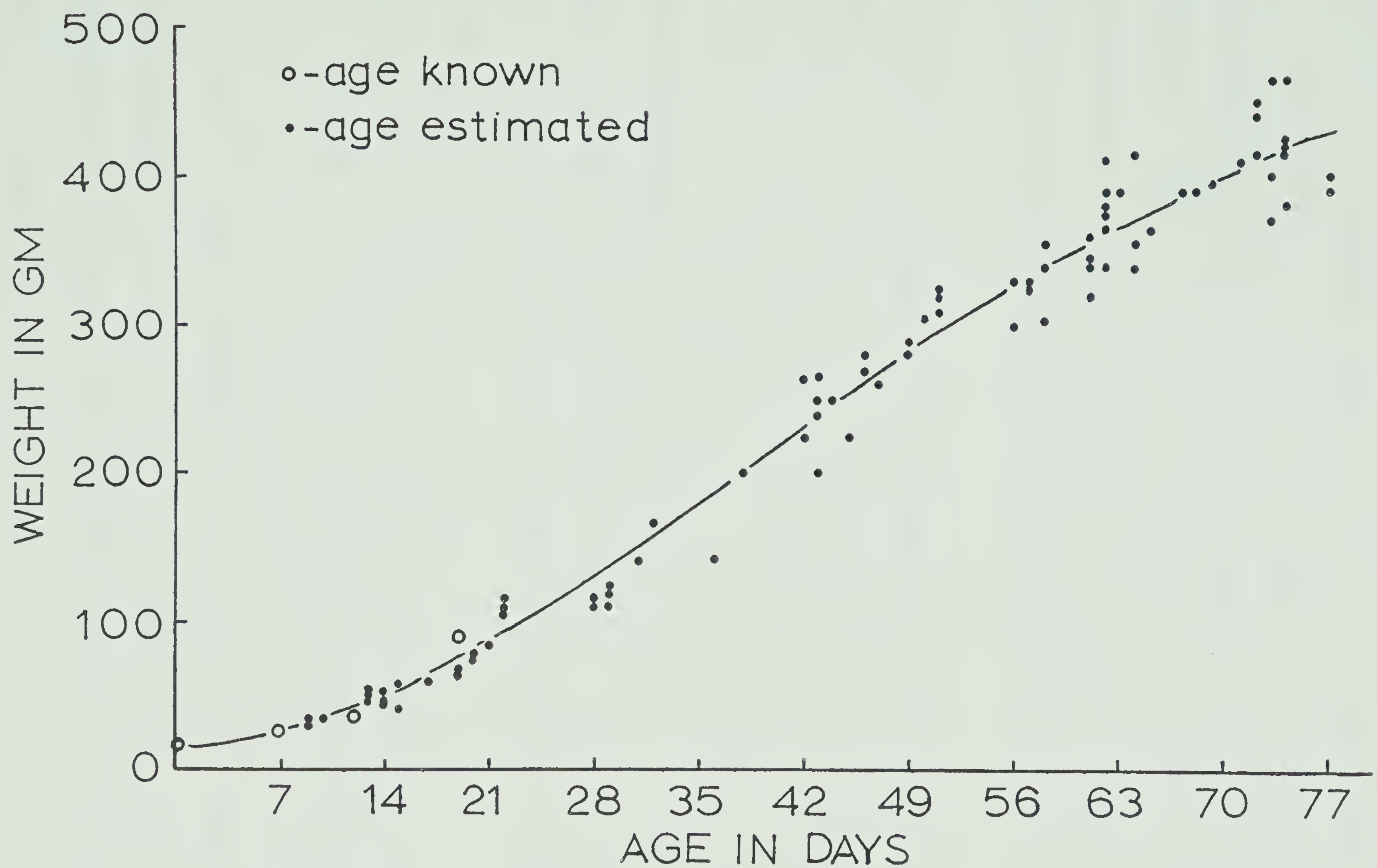

o-age known
•-age estimated
WEIGHT IN GM
500
400
300
200
100
0
7
14
21
28
35
42
49
56
63
70
77
AGE IN DAYS

Figure 11. Growth curves for body-weight of juvenile female Franklin's grouse in southwestern Alberta. The mean weights of 12 birds of known age but unknown sex are plotted on the graph. These mean weights were for all birds captured on a particular day. In addition, the graph includes 85 weights of 52 birds.



∘-age known
•-age estimated
WEIGHT IN GM
500
400
300
200
100
0
7
14
21
28
35
42
49
56
63
70
77
AGE IN DAYS

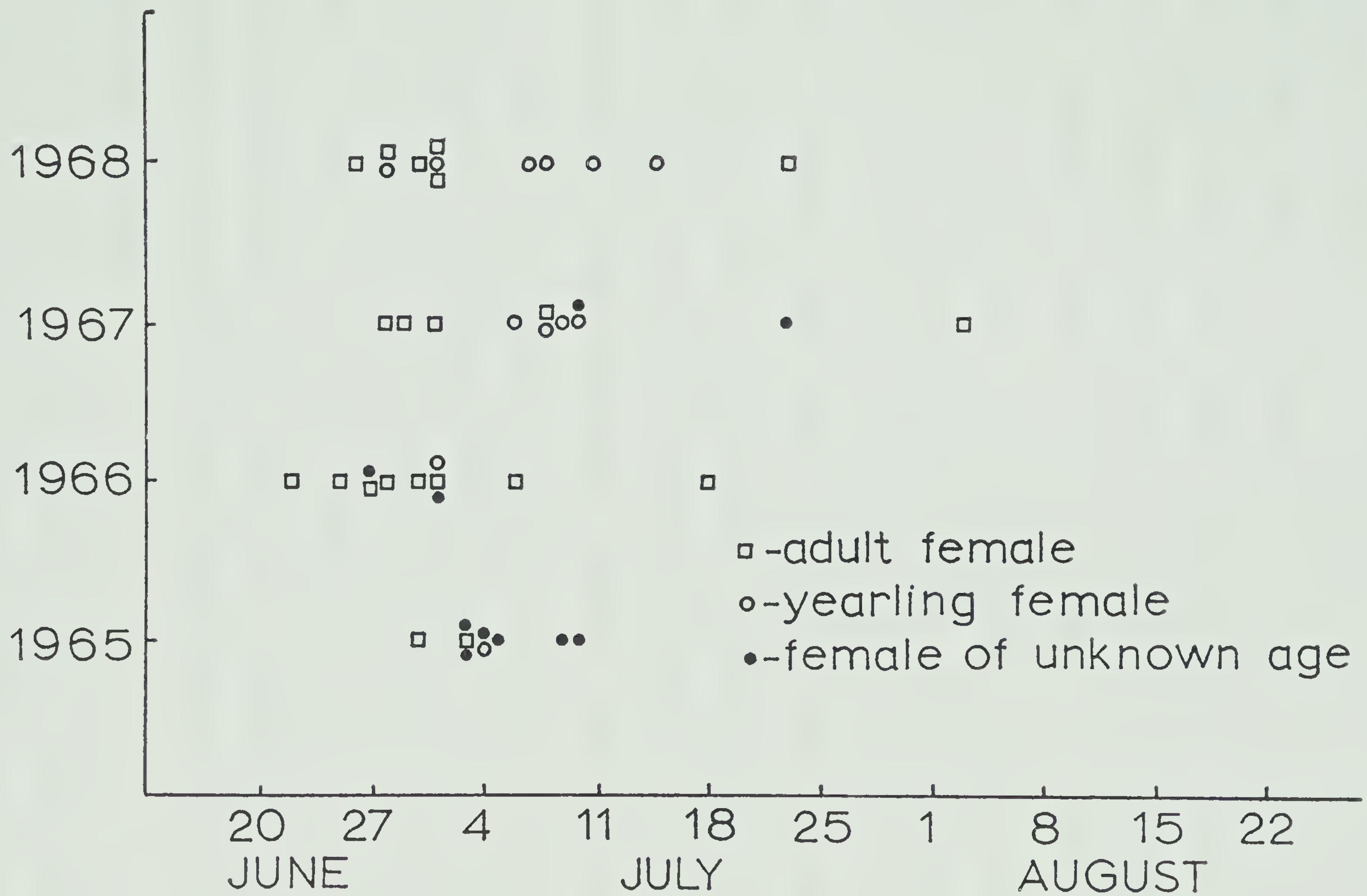
By means of the technique for determining the age of juvenile Franklin's grouse, the dates of hatching were determined for 43 broods found on the main study area between 1965 and 1968 (Figure 12). These data show that hatching occurred during a six-week period between June 22 and August 3. However, 77% of the clutches hatched within a two-week period between June 28 and July 11. On the average, 84% of the hatch in any year occurred within two weeks of its commencement.

The data in Figure 12 show that in 1966 and 1968 hatching occurred earlier than in 1965 and 1967. After combining the data for 1966 with those for 1968 and the data for 1965 with those for 1967, a Chi-square test showed a significant difference between the two resulting sets of data. Late dates of hatching result from a delay in breeding. This delay may be related to a late snow cover in 1965 and 1967 as compared with the other years.

Analyzing the dates of hatching according to the age of the hen reveals the tendency for adult females to nest earlier and continue nesting longer than yearling females. Zwickel (1965) noted the same tendency in blue grouse. The late dates of hatching shown in Figure 12, i.e. those from July 18 on, are thought to represent successful attempts at re-nesting. All birds involved were adults.

Extrapolating from dates of hatching, laying and incuba- periods can be determined based on the length of time required by a female Franklin's grouse to lay and incubate an average

Figure 12. Time of hatching in spruce grouse based on the measurements of primaries of juveniles. The symbols in the graph represent the date of hatching of clutches layed by adult and yearling females and females of unknown age.


1968
1967
1966
1965
▫-adult female
∘-yearling female
•-female of unknown age
20 27 4 11 18 25 1 8 15 22
JUNE
JULY
AUGUST

clutch of eggs.

The clutch size for spruce grouse according to Rand (1947) and Godfrey (1966) varies from 4 to 7 eggs. This variation agrees fairly well with what was found in this study. Three nests were found during the four year period. They had six, five, and three eggs, respectively. Two broods of six juveniles were observed but no brood was seen with more than six. Based on observations of one nest found in 1968 with the first egg in it, approximately 1.5 days per egg were required to complete a clutch of five. The incubation period based on observations of the same nest was 23.5 days. A full clutch of six eggs was found in 1967. Five of these eggs hatched 21 days later. These data on the interval between eggs and incubation period are very similar to those for other species of galliforms (Leopold, 1948). With these data as a basis, it would take approximately 31 days or one month to lay and incubate an average clutch of eggs. This puts the laying period approximately one month before the hatching period. Most of the laying would, therefore, begin during the two weeks between May 28 and June 11. Incubation would begin approximately eight days after commencement of laying.

Reproductive Success

Since it will be shown that reproductively unsuccessful hens have a different pattern of dispersion than successful ones, an adequate description of dispersion should include an indication of the numbers of hens in each category. Reproductively unsuccessful hens were so categorized if they were

seen without a brood; successful hens were those with a brood.

The data on reproductive success of females on the study area are presented in Table 15.

Chi-square tests showed no difference in the ratios of successful to unsuccessful hens between years. The combined data for the four years shows that 42% of the females were successful. This figure represents a minimum for the percentage of successful females.

Some of the females seen earlier in the year but which were not seen during the brood season may have had broods. A second method of evaluating reproductive success is to compare the numbers of observations of hens with broods to the number without broods during the brood period. For the purpose of this study, the brood period has been designated as the period between July 1 and September 15. From 1965 to 1968 the total number of different females with broods seen on the study area was 43 and the total seen without broods was 26. In other words, 62% of the females seen were successful. Hens with broods are probably easier to find than hens without broods. Hens with young broods exhibit a distraction display when closely approached which also increases the chances of seeing a hen with a brood as opposed to one without. The figure of 62% hens with broods is therefore likely to be a maximum. With a minimum of 42% of the females being successful and a maximum of 62%, the actual ratio of successful hens to unsuccessful hens is in the vicinity of 50:50. These results are identical to those found for blue grouse on Vancouver Island by Zwickel (1965).

Table 15. Reproductive success of female Franklin's grouse in southwestern Alberta.

	Successful Females				Unsuccessful Females			
Year	Yearlings	Adults	Age ?	Total	Yearlings	Adults	Age ?	Total
1965	1(50)*	3(100)	5(62)	9(69)	1(50)	0(0)	3(38)	4(31)
1966	1(20)	8(42)	2(40)	11(38)	4(80)	11(58)	3(60)	18(62)
1967	4(40)	5(31)	2(5)	11(37)	6(60)	11(69)	2(50)	19(63)
1968	6(40)	7(41)	0(0)	13(41)	9(60)	10(59)	0(0)	19(59)
Total	12(37)	23(42)	9(53)	44(42)	20(63)	32(58)	8(47)	60(58)

* Figures in brackets are percentages of total for each age category.

The data combined for the four years in Table 15 according to age of the female suggest that adult hens were more successful at producing a brood than yearling hens. The difference in success between the two age classes is not statistically significant. However, 45% of the 26 different females seen without broods in the brood periods of 1965-1968 were yearlings. This is a higher proportion of unproductive yearlings than would be expected if they were as capable of reproduction as adults, since yearlings comprise only 37% of the total female population. This suggests that some difference in reproductive capability between yearlings and adults may exist. A possible explanation for this difference is that adults are physiologically more capable of nesting or re-nesting than yearlings. Since hypertrophy of the ovary and reproductive tract in breeding females would increase their weight, the physiological capability of reproduction may be reflected in the body weight of the birds. A comparison of the weights of adult and yearling females in May and July is given in Table 16.

Although the differences between mean weights of adult and yearling females in both May and July appear to be substantial, they are not statistically significant. This is likely the result of the small sample size. The drop in weight from May to July for both age classes is significant. The fact that the metabolic requirements of reproduction leave

yearlings at a lower body weight than adults may preclude re-nesting attempts by the former.

Table 16. Weights of female Franklin's grouse snared on the main study area during May and July.

	May		July*	
	Adult	Yearling	Adult	Yearling
Number of birds	9	12	12	7
Mean weight	548.9g	514.2g	434.3g	410.7g
Range of weights	500-590g	450-570g	385-510g	380-480g
Standard deviation	38.5g	38.3g	33.4g	33.5g

* Only weights of females with broods in July are considered.

The apparent difference in reproductive success between yearling and adult females may also reflect a difference in their capability of breeding. Some yearling females may be less capable of breeding as a result of a lack of sexual maturation. The lower mean weight in May of yearlings as compared to adults may indicate that this is the case. Three yearling females captured on July 11, 1968 had no evidence of a brood patch. Breeding among yearlings may also be curtailed by territorial behavior of adult females (see discussion to follow). Adult females may prevent access of other females to a male's territory.

Influence of the Stage of Reproductive Cycle on Dispersion

Two factors which could logically change with the stages of the reproductive cycle and perhaps influence dispersion are

intraspecific interaction and habitat requirements. Changes in either of these factors would result in changes in the pattern of dispersion.

Interaction Between Females

Aggressive behavior between male galliforms during the breeding period has been well documented. Among spruce grouse, this behavior has been studied by Lumsden (1961), Ellison (1968), Stoneberg (1967), and McLachlin (in prep.). Aggression between females during the breeding season has been noted in red grouse (Jenkins et al., 1963), in blue grouse (Stirling, 1968), and in Franklin's grouse (MacDonald, 1968). MacDonald, (1968:8) who studied behavior of Franklin's grouse in the same population of birds that I studied, recorded "aggressive vocalizations of a female while she attacked the mounted skin of a female Franklin's grouse". He discovered that females responded aggressively to the recording of this vocalization prior to the onset of incubation. He suggests that this reaction would have a dispersive effect on the females.

In 1967 and 1968 between May 4 and June 1, seven adult and five yearling females were observed responding aggressively to a recorded call. One adult female responded to the recording as late as June 20. On May 23, 1968 two females responded simultaneously to the recording. One, an adult, approached the play-back apparatus to within 5 m. The other, a yearling, would not come closer than approximately 50 m. Two yearling females were seen together on May 5, 1968 ex-

hibiting no overt reaction to each other. An identical situation was observed with an adult and a yearling on May 7, 1968. These observations may indicate that the period of aggressiveness between females begins in early May and that some become aggressive earlier than others.

MacDonald (1968) stated that after the hatching period, females with broods may be found in proximity to each other without apparent evidence of aggression. Only twice during this study were broods seen in close proximity. No apparent aggression was observed. In addition, two observations were recorded of a broodless yearling female accompanying a second female with a brood. The females involved were different in each case. No apparent aggression was observed.

Interaction Between Males and Females

One might expect interaction between female and male Franklin's grouse to be more prevalent during the breeding season (period between May 1 and June 15) than during the remainder of the summer. One method of determining whether this is in fact the case is to compare the proportions of the observations of females with males (i.e. within 10 m of each other and each apparently aware of the other's presence) in the breeding period with those during the rest of the summer.

During the breeding period, observations of females that were with a male included 30% of a total of 93 sightings. Of 180 observations of females over the remainder of the year, only 17 or 9% of these were with males. The difference in

the proportion of females seen with males in the two periods is significant. The reason for the greater proportions of females being with males in the breeding season may be that the females are attracted to males or males are attracted to females. Stoneberg (1967) and McLachlin (in prep.) have suggested that the wing-clap display of male Franklin's grouse attracts females. Several observations during this study show that males are attracted to the flight sounds of a female.

A closer examination of the data on observations of females with males reveals that during the breeding period 32% of the adult females observed were with a male. Only 24% of the yearling females observed were with a male. The difference, though not statistically significant, suggests that yearlings may not be as successful as adults at being with a male during this period. During the rest of the summer, the difference in the percentage of observations with a male between yearlings and adults was only one per cent.

A second method of evaluating the degree of interaction between females and males is to determine how close females are to the centre of activity of a male's territory. Using an aerial photograph, I measured the distance from the location of an observation of a female to the centre of activity of the nearest male's territory. Measurements were done only if the position of the centre of activity of the nearest male's territory was reasonably certain. Information on the positions of activity centres of males was supplied by

McLachlin (unpublished data). The results are shown in Table 17.

Table 17. Distance of females from closest activity centres of male Franklin's grouse in southwestern Alberta.

	Age	Sample Size	Mean(m)	Range(m)	Standard Deviation (m)
Breeding Period	A	51	142	17- 565	116.0
	Y	34	248	0-1,220	230.4
Summer with Brood	A	68	248	35- 770	167.4
	Y	24	386	82- 835	204.4
Summer without Brood	A	25	227	65- 617	147.8
	Y	11	346	170- 670	159.0

A - Adult
Y - Yearling

Both yearling and adult females are found significantly closer to the centre of males' territories in the breeding period than in summer when the females have a brood. Adults found in the summer without a brood were significantly farther from males' territories than they were in the spring. However, this was not true for yearlings even though the difference in the mean distances was about 100 meters. These data may indicate that during the breeding period, females or males are more attracted to grouse of the opposite sex than in the summer. It is also possible that the two sexes are attracted to similar areas in terms of vegetative cover, and thus indirectly to each other. Females may be attracted to the same area in which the males are found, and once there, the males

are attracted to the females. The most common hypothesis that has been presented is that it is the females which are attracted to the males and not vice versa (Stoneberg, 1967; McLachlin, in prep.).

In each of the three cases considered in Table 17, adults are significantly closer to the centre of a male territory than are yearlings. This provides further evidence that on the average, yearlings are less successful than adults at interacting with males. If males were attracted to females then it would seem unlikely that there would be a difference between adult and yearling females in the distance from activity centres of males in the breeding period unless some other age correlated factor was involved. Yearlings may be less attracted to males, or, in view of the aggressive behavior of females towards each other during the breeding period, it is possible that at least some yearlings are repelled from a male's territory by adult females. The fact that even after the breeding period, yearlings are still farther from males' territories than adults may simply reflect the locality of the home range selected in the spring. Yearlings, which represent new members added to the population, probably select their home range in the breeding period since this is the period of aggressive behavior between females. Observations of yearling females are on the average farther from males' territories than observations of adults. Although the home range may expand in size after the breeding period, its general locality may not change. As a result, locations of

observations of yearling females are on the average consistently farther than those of adults from males' territories throughout the summer. In addition to this, it has been shown that yearlings wander more than adults. This may add to the greater average distance of yearlings from territories of males.

The lower success of yearling females than adults at interacting with males during the breeding period may be related to the lower productivity of yearlings.

Habitat and Dispersion

The description of the study area revealed the occurrence of a variety of habitat types thereon. In addition, within each habitat type there was a good deal of variability in each of the parameters measured at each site of vegetation analysis. This presented an opportunity for habitat selection by the grouse studied.

The primary objective of this study of habitat selection by female Franklin's grouse was to describe the habitat selected by the birds in terms of vegetation. It was also desirable to determine what effects the age of the female and the reproductive cycle had on the habitat selected.

Vegetation and Dispersion

Although a few sightings of females were made in the poplar and spruce forest types, the great majority of the observations were recorded in the pine forest. It was shown

in the description of the study area that spruce forest and poplar forest types comprised approximately 3.5% and 17.5% of the total study area respectively. Based on observations of the grouse over four summers, by drawing a line around the outside points of observation, females were estimated to have been found in approximately 5% of the spruce forest and 8% of the poplar forest types. Therefore, use of forest types other than pine by the females was considered negligible. Within the pine forest, females were restricted to certain areas. I estimated that females used approximately 40% of the available lodgepole pine forest. An attempt was made to discover the differences if any in the characteristics of the vegetation in the occupied and unoccupied areas of the pine forest.

As has been mentioned in the sections on methods, a series of vegetation analyses were done at random locations over the study area. The data were separated into two lots according to whether they were recorded for plots in the occupied or unoccupied areas of the pine forest. The data for canopy coverage have been recorded for each area as the total number of each of the coverage values which were assigned for each species and the total vegetation in all plots (see Appendices 5 and 6). A statistical comparison of the two sets of data was done by comparing the distribution of the coverage values for each species of plant in the different areas. For this comparison, r x 2 or 2 x 2 contingency tables were constructed (Steel and Torrie, 1960). A Chi-square test of independence was applied to the tables. The results of this test

are presented in Table 18.

The canopy coverage of Pinus contorta, Salix sp., and total vegetation in the overstory was significantly greater in the area of the forest where females were found than in the area where they were not found. In the area where females were found, the most common cover values of Pinus contorta and total cover were three and four (Appendix 6). In the areas where females were not found, the most common cover values were two and three (Appendix 5). The fact that Salix sp. was present in a relatively small number of the plots and that when it was present it had only low cover values would suggest that the difference in its abundance in the two areas may not be important.

In the middlestory, the canopy coverage of Alnus crispa was significantly less and of Salix sp. greater in the forest where females were found than where they were not found. Total middlestory cover was less in the area used by grouse than in the unoccupied area.

To summarize, the evidence shows that the vegetation in the area used by the females afforded greater canopy coverage at the overstory level and less coverage at the middlestory level than in the unoccupied areas.

By far the most common species in the overstory was Pinus contorta. Pine needles are important in the diet of spruce grouse in some areas (Crichton, 1963; Pendergast, 1969). There are indications that pine needles are also important in the diet of the grouse studied here. A possible reason for

Table 18. Statistical comparison of the distribution of cover values recorded for vegetation in 111 random plots in the pine forest where female Franklin's grouse occur and 114 random plots in the area of the pine forest where they do not occur.

Species	Overstory			Middlestory		
	x^2 tabled - 0.05 (df)	x^2 calculated	Abundance	x^2 tabled - 0.05 (df)	x^2 calculated	Abundance
Picea glauca	5.99 (2)	0.09		3.84 (1)	0.96	
Pinus contorta	7.81 (3)	36.86 *	+	3.84 (1)	1.04	
Populus balsamifera	3.84 (1)	0.14		3.84 (1)	.10	
Populus tremuloides	3.84 (1)	0.23		5.99 (2)	.04	
Salix sp.	3.84 (1)	5.22 *	+	3.84 (1)	13.93 *	+
Alnus crispa				7.81 (3)	8.44 *	-
Betula glandulosa				3.84 (1)	.00	
Potentilla fruticosa				3.84 (1)	.00	
Rosa sp.				3.84 (1)	.01	
Shepherdia canadensis				3.84 (1)	.81	
Total	7.81 (3)	41.03 *	+	7.81 (3)	15.25 *	-

* Significantly different; + = greater, - = less cover in area where grouse found

the selection of the lodgepole pine forest type by the grouse considered in this study may be that they seek pine for food.

In the middlestory, canopy coverage of _Alnus crispa_ was greater in the area where grouse were not found than in the area where they were found. _Alnus crispa_ often occurred in very dense stands on steep north-facing slopes. The comparison of slope of the terrain in the two areas will show that grouse did not live in the areas where the slope was steep. This explains the greater cover of _Alnus crispa_ in areas where the grouse were not found. _Salix sp_. had greater coverage where the grouse were found. This may reflect the better growing conditions and poor drainage on the gentler slopes where grouse were found as compared with the area where they were not found.

The average height of the canopy of the overstory vegetation was measured at each random location at which a vegetation analysis was done. The results are presented in Table 19.

Table 19. Comparison of mean canopy height of overstory vegetation on random plots in the areas where female Franklin's grouse were, and were not found.

	Occupied Area	Unoccupied Area
Sample Size	111	114
Mean Canopy Height (m)	8.06	6.85
Standard Deviation (m)	1.47	2.03

The mean canopy height of the overstory vegetation in the

area occupied by grouse was significantly greater than in the unoccupied area. It will be shown later that the slope in the area unoccupied by grouse was greater than in the area occupied. Possibly better drainage, poorer soils, and greater exposure to wind on the steeper slope resulted in inferior growth conditions for the trees in such an area. Hence the shorter trees in the area where grouse were not found. The trees may have been younger although core samples were not taken to verify this.

The density of the trees in the overstory was recorded at each of the locations where random vegetation analyses were done. The results are presented in Table 20. Since the species Salix sp., Populus balsamifera, and Populus tremuloides were found in so few of the plots, data on their densities were not included in the table.

Table 20. Comparison of density of trees in the overstory on random plots in areas where female Franklin's grouse were, and were not found.

	Pinus contorta		Picea glauca		Total	
	R-1	R-2	R-1	R-2	R-1	R-2
Sample Size	111	114	111	114	111	114
Mean Density (trees per plot)	24.77	14.05	1.44	1.81	28.20	17.85
Standard Deviation	16.53	17.18	2.34	5.19	17.22	19.25
Mean Density (trees per hectare)	4,954	2,810	288	362	5,640	3,570
Mean Density (trees per acre)	2,006	1,138	117	147	2,283	1,445

R-1 - Random plots in the area where females were found
R-2 - Random plots in the area where females were not found.

Table 20 shows that in the area occupied by grouse, approximately 90% of the trees were _Pinus contorta_, whereas in the area unoccupied by grouse they constituted approximately 80%. The density of _Pinus contorta_ and total trees in the area where grouse were found was significantly greater than the density in the area not utilized by grouse. In view of the fact that the analysis of canopy cover showed that cover was greater for _Pinus contorta_ and total vegetation in the area occupied by grouse, these results on density of the trees are not unexpected.

Stoneberg (1967) in his study of Franklin's grouse in north-western Montana divided his study area into three zones according to tree density. The density in his 'open' zone had up to 2,500 trees per acre, the 'medium' zone had from 2,500 to 5,000 trees per acre, and the 'thick' zone - densities over 5,000 trees per acre. He noted that broodless adult females were found in the 'thick' or 'medium' zones but avoided the 'open' zones. He found that hens with broods occupied the 'open' zone. The grouse in this study lived in an area which on the average corresponded to Stoneberg's 'open' zone. It will be shown later that within the area where females were found, broodless females occurred in areas with heavier cover and therefore probably denser stands of trees than females with broods. In view of this, the density of trees in the habitat selected by the two populations (i.e. N. W. Montana and S. W. Alberta) of Franklin's grouse was probably not very different.

Robinson (1969) reported that spruce grouse in northern Michigan were found at sites where the density of trees was lower than on the area as a whole. His results cannot be compared directly to those reported in this study because Robinson counted only trees with a diameter of at least 4 inches.

The diameters of the trees in all random plots were measured at breast height. Since the trees other than Pinus contorta were very sparse, their diameters did not likely influence habitat selection. The mean diameter of Pinus contorta in the area where grouse were found was 5.85 cm which compared with 5.71 cm in the unoccupied area. Because of the small difference, it is doubtful that diameter of trees influenced habitat selection by the female Franklin's grouse. The diameters of the trees on Stoneberg's (1967) and Robinson's (1969) study areas were greater than the diameters of trees on my study area. The differences are probably a reflection of the age of the trees. Stoneberg (1967) noted that the circumference of trees on his study area decreased as the density increased. In this study it has been shown that the portion of the study area unoccupied by grouse had a lower mean density of trees than the occupied area yet the mean diameter of trees on the unoccupied area was slightly lower than the mean diamter of trees on the occupied area. This is probably a reflection of the poorer growth conditions for trees on the unoccupied area resulting from a steeper slope of the terrain.

The results of the measurements of slope at each of the random plots are shown in Table 21.

Table 21. Comparison of slope of the terrain at random plots in areas where female Franklin's grouse were, and were not found.

	Occupied Area	Unoccupied Area
Sample Size	111	114
Mean Slope(°)	6.95	11.31
Standard Deviation (°)	4.60	6.39

The slope of the terrain was statistically significantly less in the area occupied by grouse than in the area where absent. It has already been mentioned that where the slope is steep possible lack of water imposed by improved drainage and greater exposure to wind may limit the growth of trees. This could explain the smaller, less dense trees in the area unoccupied by grouse as compared to the occupied areas.

In summary, it was found that the characteristics of the pine forest on the study area where female grouse were found differed from those on the area unoccupied by grouse in the following ways: on the average, canopy cover of overstory was greater and middlestory less; canopy height, diameter, and density of the treeswere greater; and the slope of the terrain was less steep. I do not know which of these factors is the most important in affecting the selection of habitat on the study area by the grouse. However, in the area occupied by the grouse, canopy coverage and associated density tended to be

more heterogeneous than canopy height, tree diameter, or slope. Thus, in comparing vegetation selected by different age and reproductive categories of females, only canopy coverage was considered.

Vegetation, Age of the Bird, and Dispersion

Female Franklin's grouse were dispersed throughout a portion of lodgepole pine forest in which certain characteristics of the vegetation differed from those in the portion of the forest uninhabited by the grouse. In determining what portion of the forest was inhabited, sightings of both yearling and adult females throughout the spring and summer were considered. The question arises as to whether the grouse were dispersed randomly throughout the occupied area or if instead they selected certain areas in terms of canopy cover of the overstory and middlestory. In addition, it was desirable to determine whether the age of the bird and stage of reproductive cycle influenced the type of habitat selected. First, an attempt will be made to answer the questions of whether the birds selected specific habitats within the occupied area and the effect of the age of the bird on this selection.

Vegetation analyses were done as described under methods at locations where birds were seen. The cover characteristics of the vegetation recorded at these sites was assumed to be the cover actually being used by the grouse. Since the female

grouse encountered in this study rarely flushed or even ran off at the approach of an observer this assumption is probably valid.

It will be shown later that different stages of the reproductive cycle have definite effects on vegetation selected by female grouse. For this reason, results of vegetation analyses done at sites where females in different reproductive categories were sighted will be compared separately with the results of the random analyses in the area occupied by grouse.

Table 22 compares the vegetation cover on random plots in the area where females were found with the cover at sites where adult females were seen during the breeding period.

In the overstory, canopy cover provided by *Populus balsamifera* was significantly less in the general area where females were found than at sites where adults were seen during the breeding period. However, it is also evident that *Populus balsamifera* was present in very few plots (Appendices 6 and 7). It is therefore unlikely that cover provided by this species of tree was important in habitat selection by adult females in the breeding period. The lack of statistically significant differences in the cover of the other species in the overstory between the two categories would suggest that adult females in the breeding period are dispersed randomly in terms of the overstory vegetation over the general area in which females were found.

In the middlestory, cover provided by *Salix sp.*, *Potentilla fruticosa*, and *Shepherdia canadensis* was significantly less in

Table 22. Statistical comparison of the cover on 111 random plots in the general area where females were found with the cover at 56 sites where adult females were seen during the breeding period.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	5.21		3.84 (1)	0.77	
Pinus contorta	5.99 (2)	0.50		3.84 (1)	0.66	
Populus balsamifera	3.84 (1)	6.39 *	-	3.84 (1)	0.03	
Populus tremuloides	3.84 (1)	0.63		3.84 (1)	0.14	
Salix sp.	3.84 (1)	2.24		5.99 (2)	7.14 *	-
Alnus crispa				5.99 (2)	0.15	
Betula glandulosa				3.84 (1)	0.07	
Potentilla fruticosa				3.84 (1)	8.58 *	-
Rosa sp.				3.84 (1)	1.44	
Shepherdia canadensis				3.84 (1)	5.57 *	-
Total	5.99 (2)	1.60		3.84 (1)	1.90	

* Significantly different; + = greater, - = less cover in area where grouse found

the general area where females were found than at sites where adults were seen during the breeding period. A comparison of Appendices 6 and 7 shows that Potentilla fruticosa and Shepherdia canadensis were present in relatively few plots and were therefore probably not important in habitat selection.

Table 23 shows a comparison of the cover on random plots in the area where females were found with the cover at sites where yearling females were seen during the breeding period. There are no statistically significant differences between cover available to the yearlings in the area where females lived and that specifically selected by them.

It appears then that on the whole, both adults and yearlings do not select cover in the area in general where they live which differs greatly from that which is available to them. This also suggests that adults do not select cover which is very different from that which yearlings select. In an attempt to examine the effect of age of the bird on habitat selection in the breeding period I compared cover characteristics of the vegetation at sites where each of the two categories of females were seen.

Table 24 shows the results of the comparison of the cover selected by adult females with that selected by yearling females. There are no significant differences in the cover selected by the two age categories of females.

Summarizing the results presented so far, it appears that during the breeding period adult and yearling females select similar vegetative cover and that this cover does not differ

Table 23. Statistical comparison of the cover on 111 random plots in the general area where females were found with the cover at 24 sites where yearling females were seen during the breeding period.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated
Picea glauca	3.84 (1)	0.30	3.84 (1)	1.76
Pinus contorta	5.99 (2)	2.54	3.84 (1)	0.04
Populus balsamifera	3.84 (1)	0.07	3.84 (1)	0.00
Populus tremuloides	3.84 (1)	1.10	3.84 (1)	0.39
Salix sp.	3.84 (1)	1.22	3.84 (1)	0.02
Alnus crispa			3.84 (1)	1.56
Betula glandulosa			3.84 (1)	0.72
Potentilla fruticosa			3.84 (1)	0.72
Rosa sp.			3.84 (1)	0.01
Shepherdia canadensis			3.84 (1)	0.57
Total	3.84 (1)	1.35	3.84 (1)	0.06

Table 24. Statistical comparison of the cover at 56 sites where adult females were seen during the breeding period with the cover at 24 sites where yearling females were seen during the breeding period.

Species	Overstory		Middlestory	
	x^2 tabled - 0.05 (df)	x^2 calculated	x^2 tabled - 0.05 (df)	x^2 calculated
Picea glauca	3.84 (1)	3.29	3.84 (1)	0.24
Pinus contorta	5.99 (2)	1.03	3.84 (1)	0.80
Populus balsamifera	3.84 (1)	1.91	3.84 (1)	0.02
Populus tremuloides	3.84 (1)	0.00	3.84 (1)	1.02
Salix sp.	3.84 (1)	0.02	3.84 (1)	0.01
Alnus crispa			3.84 (1)	1.29
Betula glandulosa			3.84 (1)	0.19
Potentilla fruticosa			3.84 (1)	1.91
Rosa sp.			3.84 (1)	0.63
Shepherdia canadensis			3.84 (1)	3.94
Total	3.84 (1)	0.15	3.84 (1)	0.12

greatly from that which was available in the general area where grouse were found. Because of the fact that vegetation selected by adults and yearlings was similar and the small sample size especially of vegetation analyses done for yearling females, data for all birds were pooled and compared to the random vegetation analyses done in the area utilized by grouse.

Table 25 shows the statistical comparison of cover selected by all females during the breeding period with that which was available in the area where females were found. The total overstory cover was significantly greater at sites where females were seen. The fact that when cover selected by adult and yearling females was compared separately to the cover available no statistically significant difference occurred for total overstory cover indicates that the sample size for each age category may have been too small.

In the middlestory, cover provided by <u>Salix</u> <u>sp</u>. and <u>Potentilla</u> <u>fruticosa</u> was significantly greater at sites where females were seen. Since <u>Potentilla</u> <u>fruticosa</u> was present in relatively few plots (See Appendices 6 and 9) it was probably unimportant in habitat selection. <u>Salix</u> <u>sp</u>. however, may have been important. But since total middlestory cover did not differ for the two groups, this is unlikely.

On the basis of the results presented above, one can conclude that during the breeding period, female Franklin's grouse selected cover which did not differ greatly from that which was available in the area where grouse were found. Perhaps they selected a greater total overstory cover. The habitat

Table 25. Statistical comparison of the cover on 111 random plots in the general area where females were found with the cover at 80 sites where adult and yearling females were seen during the breeding period.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	2.27		3.84(1)	1.91	
Pinus contorta	5.99 (2)	1.67		3.84 (1)	0.11	
Populus balsamifera	3.84 (1)	3.57		3.84 (1)	0.14	
Populus tremuloides	3.84 (1)	1.50		3.84 (1)	0.08	
Salix sp.	3.84 (1)	3.06		5.99 (2)	6.41 *	+
Alnus crispa				5.99 (2)	1.97	
Betula glandulosa				3.84 (1)	0.24	
Potentilla fruticosa				3.84 (1)	5.32 *	+
Rosa sp.				3.84 (1)	0.68	
Shepherdia canadensis				3.84 (1)	2.21	
Total	7.81 (3)	14.73 *	+	5.99 (2)	2.07	

* Significantly different; + = greater cover at sites where adult and yearling females were seen.

selected by adult females did not differ significantly from that selected by yearlings.

Very few females were seen in the period of time between the end of the breeding period (June 15) and the time when broods first started to appear (approximately July 1). Therefore, there was not enough data on habitat selection at this time to warrant statistical treatment of it.

Females seen during the period of time between July 1 and September 15 were grouped into two reproductive categories: those with broods and those without broods. The habitat selection will be examined first for females seen with broods.

A statistical comparison of the cover available in the area where females were found with that specifically utilized by adult females seen in the summer with a brood is shown in Table 26. Cover provided by _Pinus contorta_ was significantly less and that by _Populus balsamifera_ and _Populus tremuloides_ greater where adult females with broods were seen than that which was available to the birds. Because _Populus balsamifera_ and _Populus tremuloides_ were present in very few plots (see Appendices 6 and 10) the importance of them in habitat selection is questionable. The difference in the total overstory cover for the two groups of data is not statistically significant although it is close to being so. Comparing Appendix 6 and 10 shows that cover values for the total overstory are on the average slightly lower where adult females were seen with broods than in the general area where females were found.

In the middlestory, Table 26 shows statistically signif-

Table 26. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 70 sites where adult females with broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	0.88		3.84 (1)	9.80 *	+
Pinus contorta	5.99 (2)	8.15 *	-	3.84 (1)	1.87	
Populus balsamifera	3.84 (1)	7.36 *	+	3.84 (1)	11.52 *	+
Populus tremuloides	3.84 (1)	5.89 *	+	3.84 (1)	15.06 *	+
Salix sp.	3.84 (1)	1.72		7.81 (3)	81.78 *	+
Alnus crispa				5.99 (2)	2.45	
Betula glandulosa				3.84 (1)	6.40 *	+
Potentilla fruticosa				3.84 (1)	35.39 *	+
Rosa sp.				3.84 (1)	15.35 *	+
Shepherdia canadensis				3.84 (1)	21.75 *	+
Total	5.99 (2)	4.10		7.81 (3)	73.38 *	+

* Statistically different; + = greater, - = less cover at sites where adult females were seen with broods

icant differences for Picea glauca, Populus balsamifera, Populus tremuloides, Salix sp., Betula glandulosa, Potentilla fruticosa, Rosa sp., Shepherdia canadensis, and total middlestory. All of these species and the total provided greater cover where adult females were seen with broods. While only Picea glauca and Salix sp. were present in more than 50% of the plots (see Appendices 6 and 10) all species were probably important in contributing to a dense total cover of middlestory. The grouse may have selected the heavier middlestory because the cover provided by the overstory was relatively light. Perhaps the amounts of overstory and middlestory are inversely proportional.

Table 27 shows the results of a statistical comparison of the cover available in the area where females were found with that specifically utilized by yearling females seen in the summer with a brood. In the overstory the cover provided by Pinus contorta and Salix sp. was significantly less where yearling females were seen with broods than at random over the general area where females were found. The apparent difference in cover provided by Salix sp. is likely an artifact arising from the small sample size. The difference in the cover of total overstory although not statistically significant is almost so. Comparing Appendix 6 and Appendix 11 shows that higher cover values occurred for total overstory in the general area where grouse were found than at the sites where yearlings with broods were seen.

In the middlestory, Populus tremuloides, Potentilla frut-

Table 27. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 23 sites where yearling females with broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
<u>Picea glauca</u>	3.84 (1)	1.29		3.84 (1)	0.16	
<u>Pinus contorta</u>	5.99 (2)	8.23 *	-	3.84 (1)	1.77	
<u>Populus balsamifera</u>	3.84 (1)	1.20		3.84 (1)	0.06	
<u>Populus tremuloides</u>	3.84 (1)	0.00		3.84 (1)	9.42 *	+
<u>Salix sp.</u>	3.84 (1)	3.89 *	-	3.84 (1)	0.01	
<u>Alnus crispa</u>				3.84 (1)	0.00	
<u>Betula glandulosa</u>				3.84 (1)	0.09	
<u>Potentilla fruticosa</u>				3.84 (1)	5.96 *	+
<u>Rosa sp.</u>				3.84 (1)	4.08 *	+
<u>Shepherdia canadensis</u>				3.84 (1)	9.42 *	+
Total	3.84 (1)	2.93		3.84 (1)	12.03 *	+

* Statistically different; + = greater, - = less cover at sites where yearling females were seen with broods.

icosa, Rosa sp., Shepherdia canadensis, and total middlestory provided cover which was significantly greater at sites where yearling females with broods were seen than over the general area inhabited by females. Although none of the individual species of plants in the middlestory were present in the plots 50% of the time (see Appendix 11) they were important in contributing to the heavy cover of the total middlestory. The arguments used to explain the selection of a heavy middlestory by adult females with broods would also apply to the yearling females with broods.

The differences between the cover selected by adult females with broods and the cover characteristics of that portion of the pine forest inhabited by females generally correspond to the differences found when yearling females with broods were considered. This suggests that the two age categories of females with broods selected similar habitat with relatively light overstory cover and heavy middlestory cover. Cover selected by the two age categories of females with broods was compared. The results shown in Table 28 indicate no statistically significant differences.

The results of a comparison of cover available in the area where females were found and the pooled data for adult and yearling females seen with broods are shown in Table 29. Statistically significant differences occurred for the total overstory and all species in the overstory except Picea glauca. Cover of Pinus contorta and total overstory at specific sites where birds were seen was less than that available. For the

Table 28. Statistical comparison of the cover at 70 sites where adult females with broods were seen during the summer with the cover at 23 sites where yearling females with broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated
Picea glauca	3.84 (1)	1.63	3.84 (1)	1.71
Pinus contorta	3.84 (1)	0.29	3.84 (1)	0.03
Populus balsamifera	3.84 (1)	0.03	3.84 (1)	1.74
Populus tremuloides	3.84 (1)	0.35	3.84 (1)	0.01
Salix sp.	3.84 (1)	1.12	5.99 (2)	4.20
Alnus crispa			3.84 (1)	0.03
Betula glandulosa			3.84 (1)	0.17
Potentilla fruticosa			3.84 (1)	2.46
Rosa sp.			3.84 (1)	0.10
Shepherdia canadensis			3.84 (1)	0.01
Total	5.99 (2)	2.73	5.99 (2)	4.34

Table 29. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 110 sites where adult and yearling females with broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
<u>Picea glauca</u>	5.99 (2)	0.05		3.84 (1)	8.50 *	+
<u>Pinus contorta</u>	7.81 (3)	11.44 *	-	3.84 (1)	4.45 *	+
<u>Populus balsamifera</u>	3.84 (1)	6.26 *	+	3.84 (1)	8.41 *	+
<u>Populus tremuloides</u>	3.84 (1)	4.62 *	+	3.84 (1)	19.36 *	+
<u>Salix sp</u>.	3.84 (1)	5.34 *	+	9.49 (4)	77.01 *	+
<u>Alnus crispa</u>				5.99 (2)	1.91	
<u>Betula glandulosa</u>				3.84 (1)	4.23 *	+
<u>Potentilla fruticosa</u>				3.84 (1)	27.10 *	+
<u>Rosa sp</u>.				3.84 (1)	15.95 *	+
<u>Shepherdia canadensis</u>				3.84 (1)	20.53 *	+
Total	5.99 (2)	7.93 *	-	7.81 (3)	73.06 *	+

* Statistically different; + = greater, - = less cover where adult and yearling females with broods were seen.

other species in the overstory the opposite was true. These other species were present in relatively few plots where birds were seen (see Appendix 12) thus likely minimizing their importance in habitat selection.

In the middlestory the total and every species except Alnus crispa provided significantly greater cover at sites where birds were seen than they did over the general area as a whole.

The results presented above lead one to the conclusion that in summer, females with broods select specific areas in terms of vegetative cover within the general area inhabited by females. The habitat selected by adult females with broods did not differ significantly from that selected by yearling females with broods.

The results of a statistical comparison of the cover at points where adult females without broods were seen and the cover at random sites in the area where females were found are shown in Table 30. In the overstory Pinus contorta and total overstory provided significantly more cover at sites where females without broods were seen than at random sites in the area inhabited by females. In the middlestory, no significant differences occurred between the two groups of data. Note that the Chi-square value found for total middlest ry was almost significant at the 0.05 level. A comparison of Appendix 6 and Appendix 13 shows that the middlestory cover was heavier where adult females without broods were seen than in the general area in which females were found.

Table 30. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 19 sites where adult females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	x^2 tabled - 0.05 (df)	x^2 calculated	Abundance
<u>Picea glauca</u>	3.84 (1)	0.00		3.84 (1)	0.00	
<u>Pinus contorta</u>	3.84 (1)	16.03 *	+	3.84 (1)	0.39	
<u>Populus balsamifera</u>	3.84 (1)	0.18		3.84 (1)	0.01	
<u>Populus tremuloides</u>	3.84 (1)	0.18		3.84 (1)	0.12	
<u>Salix sp.</u>	3.84 (1)	0.42		3.84 (1)	0.09	
<u>Alnus crispa</u>				3.84 (1)	0.93	
<u>Betula glandulosa</u>				3.84 (1)	1.01	
<u>Potentilla fruticosa</u>				3.84 (1)	0.18	
<u>Rosa sp.</u>				3.84 (1)	0.01	
<u>Shepherdia canadensis</u>				3.84 (1)	0.03	
Total	3.84 (1)	14.82 *	+	3.84 (1)	3.52	

* Significantly different; + = greater cover where adult females without broods were seen.

Table 31 shows the results of a comparison of the cover at locations where yearling females without broods were seen and the cover at random sites in the area in which females were found. Populus balsamifera in the overstory provided a significantly greater amount of cover at sites where yearling females without broods were seen. A comparison of Appendix 6 and Appendix 14 shows that for both groups Populus balsamifera was present in very few plots. Therefore, it was probably not important in habitat selection.

In the middlestory Populus balsamifera, Populus tremuloides, Shepherdia canadensis and total middlestory provided significantly more cover at sites where yearling females without broods were seen than in the general area in which females were found. A comparison of Appendix 6 and Appendix 14 shows that of the above three species, all occurred in relatively few plots and were therefore probably of little significance when considered individually. Perhaps they were important in that together they contributed to a heavier total middlestory cover.

Both adult females without broods and yearling females without broods selected a relatively heavy middlestory cover. However, the data show that adults selected a relatively heavy cover of Pinus contorta in the overstory as well as total overstory. Yearlings did not show this selection. A comparison of the cover selected by the two age categories of females without broods bears this out (Table 32). Statistically significant differences occurred for Pinus contorta and total overstory.

Table 31. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 17 sites where yearling females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	3.84 (1)	2.18		3.84 (1)	0.12	
Pinus contorta	3.84 (1)	0.21		3.84 (1)	0.16	
Populus balsamifera	3.84 (1)	11.09 *	+	3.84 (1)	4.40 *	+
Populus tremuloides	3.84 (1)	0.03		3.84 (1)	6.74 *	+
Salix sp.	3.84 (1)	0.15		3.84 (1)	2.14	
Alnus crispa				3.84 (1)	0.00	
Betula glandulosa				3.84 (1)	3.60	
Potentilla fruticosa				3.84 (1)	0.24	
Rosa sp.				3.84 (1)	3.17	
Shepherdia canadensis				3.84 (1)	10.59 *	+
Total	3.84 (1)	0.15		3.84 (1)	10.31 *	+

* Statistically different; + = greater, - = less cover at sites where yearling females without broods were seen.

Table 32. Statistical comparison of the cover at 19 sites where adult females without broods were seen during the summer with the cover at 17 sites where yearling females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
<u>Picea</u> <u>glauca</u>	3.84 (1)	0.68		3.84 (1)	0.00	
<u>Pinus</u> <u>contorta</u>	3.84 (1)	13.38 *	+	3.84 (1)	0.69	
<u>Populus</u> <u>balsamifera</u>	3.84 (1)	2.93		3.84 (1)	1.71	
<u>Populus</u> <u>tremuloides</u>	3.84 (1)	0.00		3.84 (1)	2.23	
<u>Salix</u> <u>sp</u>.	3.84 (1)	0.05		3.84 (1)	1.71	
<u>Alnus</u> <u>crispa</u>				3.84 (1)	0.50	
<u>Betula</u> <u>glandulosa</u>				3.84 (1)	0.66	
<u>Potentilla</u> <u>fruticosa</u>				3.84 (1)	0.42	
<u>Rosa</u> <u>sp</u>.				3.84 (1)	1.91	
<u>Shepherdia</u> <u>canadensis</u>				3.84 (1)	1.91	
Total	3.84 (1)	5.74 *	+	5.99 (2)	1.94	

* Statistically different; + = greater cover at sites where adult females without broods were seen.

In view of the fact that no important differences were apparent in the habitat selected by adults and yearlings during the breeding period and during the summer with broods, I would not expect a difference between the cover selected by adults and yearlings without broods. Perhaps the sample size (19 for adult females and 17 for yearling females) was too small to be truly representative.

Because of the small sample size of each group of females, the data for both adult and yearling females without broods were grouped. The grouped data were then compared with data from random analyses done in the area in which females were found. The results of this comparison are shown in Table 33. The important statistically significant differences to note are those for total overstory and total middlestory. Both provided more cover at locations where females were seen without broods than at random sites in the area in which females were found.

The conclusions which can be reached from this study of the relationship of vegetation and age of bird to dispersion are as follows. Both adult and yearling females selected similar habitat in terms of cover provided by overstory and middlestory vegetation. In the breeding period, females selected cover which was not very different from that which was present on the average area inhabited by females. Females seen in the summer with broods selected a relatively light overstory and heavy middlestory. Females without broods seen in the summer selected both a heavier overstory cover and a

Table 33. Statistical comparison of the cover on 111 random plots in the area where females were found with the cover at 46 sites where adult and yearling females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	1.14		3.84 (1)	1.29	
Pinus contorta	5.99 (2)	4.28		3.84 (1)	0.30	
Populus balsamifera	3.84 (1)	4.33 *	+	3.84 (1)	1.52	
Populus tremuloides	3.84 (1)	0.13		3.84 (1)	3.43	
Salix sp.	3.84 (1)	0.24		5.99 (2)	28.89 *	+
Alnus crispa				5.99 (2)	0.20	
Betula glandulosa				3.84 (1)	2.18	
Potentilla fruticosa				3.84 (1)	2.18	
Rosa sp.				3.84 (1)	1.45	
Shepherdia canadensis				3.84 (1)	3.43	
Total	5.99 (2)	11.18 *	+	5.99 (2)	27.27 *	+

* Significantly different; + = greater cover at sites where females without broods were seen

heavier middlestory cover than that of the random sites.

It is evident that the different reproductive categories of females were seen at locations with different vegetative characteristics. Possible reasons for this and a more exhaustive examination of the influence of the stage of reproductive cycle on dispersion in terms of vegetation is the topic of the next section.

A possible bias which may have influenced the results of this section is that possibly unequal amounts of time were spent on different portions of the study area which females inhabited. This could result in the number of vegetation analyses done at sites where birds were seen being disproportionate to the number of birds actually utilizing the different portions of the area. Although this was realized, no record of time spent on different areas was kept. I believe, however, that this possible bias did not affect the results signficantly since the results presented in the following section corroborate those presented in this section.

Vegetation, Reproductive Cycle, and Dispersion

In this section, data on vegetation analyses at sightings of adult and yearling females will be grouped for two reasons. First, no conclusive evidence was found for any important differences in the habitat selected by adults and yearlings. And secondly, sample sizes of data for adults or yearlings are small.

The results presented in the preceding section indicated

that the habitat selected by females in the breeding period differed from that selected in summer when the females had broods. A comparison of the cover at sites where females were seen during the breeding period and the cover where they were seen with broods in the summer is shown in Table 34. In the overstory, statistically significant differences occurred for *Pinus contorta*, *Salix sp.*, and total overstory cover. The cover for both species and the total was greater where birds were seen during the breeding period than where they were seen with broods in the summer. In the middlestory it can be seen that statistically significant differences occurred for several species as well as the total middlestory. All these species and the total provided greater cover where females were seen with broods than where females were seen during the breeding period.

It has been shown that during the breeding period females are often seen with males. McLachlin (in prep.) has shown that the cover selected by territorial males and females during this period is similar. McLachlin (in prep.) and Stoneberg (1967) hypothesized that females are attracted to wing-clapping males during the breeding period. If this is the case, then the habitat selected by the males would have at least some effect upon the habitat utilized by females during this period.

Females seen in summer with broods selected a relatively light overstory and a relatively heavy middlestory compared to that selected in the breeding period. These results correspond with those of Stoneberg (1967). Stoneberg noted that *Vaccinium*

Table 34. Statistical comparison of the cover at 80 sites where females were seen during the breeding period with the cover at 110 sites where females with broods were seen during the summer.

Species	Overstory – x^2 tabled 0.05 (df)	Overstory – x^2 calculated	Overstory – Abundance	Middlestory – x^2 tabled 0.05 (df)	Middlestory – x^2 calculated	Middlestory – Abundance
Picea glauca	5.99 (2)	2.78		3.84 (1)	1.29	
Pinus contorta	7.81 (3)	9.75 *	+	3.84 (1)	5.59 *	-
Populus balsamifera	3.84 (1)	0.06		3.84 (1)	6.49 *	-
Populus tremuloides	3.84 (1)	0.05		3.84 (1)	14.88 *	-
Salix sp.	5.99 (2)	17.41 *	+	7.81 (3)	40.85 *	-
Alnus crispa				5.99 (2)	0.74	
Betula glandulosa				3.84 (1)	2.51	
Potentilla fruticosa				3.84 (1)	7.52 *	-
Rosa sp.				3.84 (1)	7.02 *	-
Shepherdia canadensis				3.84 (1)	6.63 *	-
Total	7.81 (3)	15.18 *	+	7.81 (3)	51.54 *	-

* Statistically different; + = greater, - = less cover at sites where females were seen during breeding period.

sp. berries were present only in the 'open' zone and that hens, in bringing off their broods on or near this area, could make use of this source of food. On my study area, Vaccinium sp. berries were not restricted to particularly open areas and were often seen at sites where broodless females were found. It has been shown that the density of trees on my study area corresponded to that on Stoneberg's 'open' zone. This may explain the more liberal distribution of Vaccinium sp. berries on my study area. However, broods were often observed eating Vaccinium sp. berries. Pendergast (1969), who studied nutrition of the spruce grouse in the Swan Hills region of Alberta, noted that in August and September new berries of Vaccinium sp. became very important in the diet of both juveniles and adults. Assuming this to be the case on my area, the distribution of Vaccinium sp. would therefore not account for the difference in cover selection between females with and without broods. This difference was indicated in the previous section and will be dealt with more, later in this section.

In his study, Pendergast found that juvenile spruce grouse consumed arthropods exclusively in the first week of their lives. During August, juveniles utilized insects more than adults. In September, the insect consumption fell to the adult level. Pendergast suggested that the utilization of insects by very young birds is probably associated with a high dietary protein requirement. Assuming that the juvenile spruce grouse in the area considered in this study are equally dependent on insect life, a possible explanation for the selection of a light over-

story and heavy middlestory cover by females with broods is as follows. Since a lighter overstory would result in less shade than in areas of heavier overstory, then conceivably it would be warmer in the areas where females with broods were seen. The warmer temperature could logically result in a more abundant and active insect life being available to the juvenile grouse in these areas. As mature females are not as dependent upon insects for food as juveniles, the question arises as to why the females would select this habitat. It is possible that the juveniles, and not the mature females are actively seeking out the habitat characterized by light overstory and heavy middlestory. Evidence of this is that when broods are watched feeding, it appeared that the hen usually followed her brood rather than vice versa.

Since the dependence upon insects by juveniles diminished as they grew older, it may be expected that their use of the habitat with light overstory would also diminish. This possibility was examined by comparing the total overstory cover selected by broods in July with that used in August and September. No statistically significant differences were found when this was done. However, when the actual amount of cover was estimated by using the midpoints in the range of percent cover which each cover value represents, it was found that there was a tendency for less use of the light overstory cover. The cover used by females with broods in July was estimated to be 35% (n=41),in August, 39% (n=42), and in September, 42% (n=27). Stoneberg (1967) also found that by the end of July broods

moved into the thicker lodgepole pine. These results support the hypothesis that broods select a light overstory cover because more food, namely insects, is available in that type of habitat. The reason for the denser middlestory may be that the less shaded area supports the growth of more middlestory plants. It could also be that since there is less overstory cover under which to hide from predators a denser middlestory is selected to counteract this. Perhaps both factors are involved.

The results in the previous section showed that while females seen during the breeding period selected cover not unlike that which was generally available to them, females seen in the summer without broods selected areas with relatively heavy overstory and middlestory cover. The results of a comparison of vegetation analyses done where birds were seen during the breeding period with those done where females without broods were seen during the summer are presented in Table 35. In the overstory, no statistically significant differences occurred between the two groups. However, the difference in selection of overstory cover was very close to being statistically significant. A comparison of Appendix 9 and Appendix 15 shows that the overstory was heavier at sites where females without broods were seen in the summer.

In the middlestory, *Salix sp.* and total middlestory provided significantly greater cover where females without broods were seen. The period of preference for more cover at both the overstory and middlestory levels coincide with the period

Table 35. Statistical comparison of the cover at 80 sites where females were seen during the breeding period with the cover at 46 sites where females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	4.07		3.84 (1)	0.02	
Pinus contorta	5.99 (2)	2.45		3.84 (1)	0.85	
Populus balsamifera	3.84 (1)	0.01		3.84 (1)	1.29	
Populus tremuloides	3.84 (1)	0.00		3.84 (1)	2.81	
Salix sp.	3.84 (1)	3.66		5.99 (2)	8.60 *	+
Alnus crispa				5.99 (2)	2.09	
Betula glandulosa				3.84 (1)	1.20	
Potentilla fruticosa				3.84 (1)	0.01	
Rosa sp.				3.84 (1)	0.08	
Shepherdia canadensis				3.84 (1)	0.08	
Total	7.81 (3)	7.79		5.99 (2)	18.97 *	+

* Significantly different; + = greater cover where females without broods were seen during the summer.

of moult. Perhaps during the moult, birds are less capable of escaping from predators, hence the preference for heavier cover.

The cover at places where females with broods were seen was compared with the cover where females without broods were seen (Table 36). The reasons for the difference in cover selection between these two reproductive categories of females have already been discussed. These results agree generally with those found by Stoneberg (1967). Ellison (from Robinson, 1969) studying spruce grouse in Alaska, also found that unproductive females selected more dense habitat than females with broods. Robinson (1969) noted however, that in Michigan, moulting birds and hens with broods were found in the same habitat.

Dispersal

Population dispersal has been defined by Odum (1953) as the movement of individuals into or out of the population. It may take three forms - emigration, immigration, or migration. In the population of Franklin's grouse I studied, no evidence was found for migration. There is, however, evidence that immigration occurs. It has been shown earlier that most of the new members of the population in the spring are yearlings. This would suggest that emigration may have occurred in the population studied. It would also suggest that if emigration occurred, it would primarily involve juveniles. In this section, the occurrence of dispersal will first be examined for the adults and yearlings and secondly for juveniles.

Table 36. Statistical comparison of the cover at 110 sites where females with broods were seen during the summer with the cover at 46 sites where females without broods were seen during the summer.

Species	Overstory x^2 tabled - 0.05 (df)	Overstory x^2 calculated	Overstory Abundance	Middlestory x^2 tabled - 0.05 (df)	Middlestory x^2 calculated	Middlestory Abundance
Picea glauca	5.99 (2)	1.16		3.84 (1)	0.76	
Pinus contorta	7.81 (3)	17.02 *	-	3.84 (1)	0.59	
Populus balsamifera	3.84 (1)	0.08		3.84 (1)	0.54	
Populus tremuloides	3.84 (1)	0.26		3.84 (1)	2.05	
Salix sp.	3.84 (1)	1.08		7.81 (3)	6.72	
Alnus crispa				3.84 (1)	0.02	
Betula glandulosa				3.84 (1)	0.03	
Potentilla fruticosa				3.84 (1)	6.16 *	+
Rosa sp.				3.84 (1)	2.66	
Shepherdia canadensis				3.84 (1)	2.36	
Total	5.99 (2)	25.45 *	-	7.81 (3)	8.48 *	+

* Significantly different; + = greater, - = less cover at sites where females with broods were seen.

Dispersal in Adult and Yearling Females

Any adult or yearling female which disappeared from the population could have either died or emigrated. A comparison of the disappearance of yearlings and adult females from my study area is presented in Table 37.

Table 37. Comparison of the disappearance of yearling and adult females from the main study area.

	Birds Marked				Birds Surviving the Following Year							
					A		Y		U		Total	
Year	A	Y	U	Total	No.	% Dis.	No.	% Dis.	No.	% Dis.	No.	% Dis.
1965	3	2	8	13			2	0	7	12.5	98	38
1966	19	5	5	29	10	47	4	20	2	60	16	46
1967	16	10	4	30	8	50	6	40	2	50	16	50
Total	38	17	17	72	18	53	12	29	11	35	41	43

A - Adult female
Y - Yearling female
U - Female of unknown age
Dis. - disappearance

Although the disappearance rate for adults is higher than that for yearlings, the difference is not statistically significant. The average disappearance rate of 43% for females compares with a mortality rate of 56% per annum that Boag (1966) calculated for yearling and adult blue grouse in southwestern Alberta.

An indication of the probablity of dispersal among yearling and adult females may be gained by measuring the distance between the centre of the points of observation of a female seen in two consecutive years. This was done with the aid of

aerial photographs. The results are shown in Table 38.

Table 38. Distance between home ranges used by females in consecutive years.

	Adult females	Yearling females	Females - Unknown Age
Sample Size	11	9	9
Mean Distance (m)	140	536	324
Range (m)	60-260	280-800	100-700
Standard Deviation (m)	69.9	180.2	178.8

Table 38 shows that yearling females move greater distances between years than adults. The difference is statistically significant. Thus, one would expect that the chance of a yearling moving out of the study area between years would be greater than the chance of an adult moving out.

It is interesting to note that the distance moved between years by adult and yearling females is relatively small when compared with the distances they move within one year. It was shown earlier that the mean longest dimension of the home range was 463 m for adults and 817 m for yearlings. This would suggest that within any year, a yearling female would be more likely to move off the study area during the period from May 1 to September 15 than during the period from September 16 to April 30.

The data on movements of females within and between years indicates that yearlings are more likely to emigrate from the study area than adults. This somewhat contradicts the results on disappearance in which adults were calculated to have a

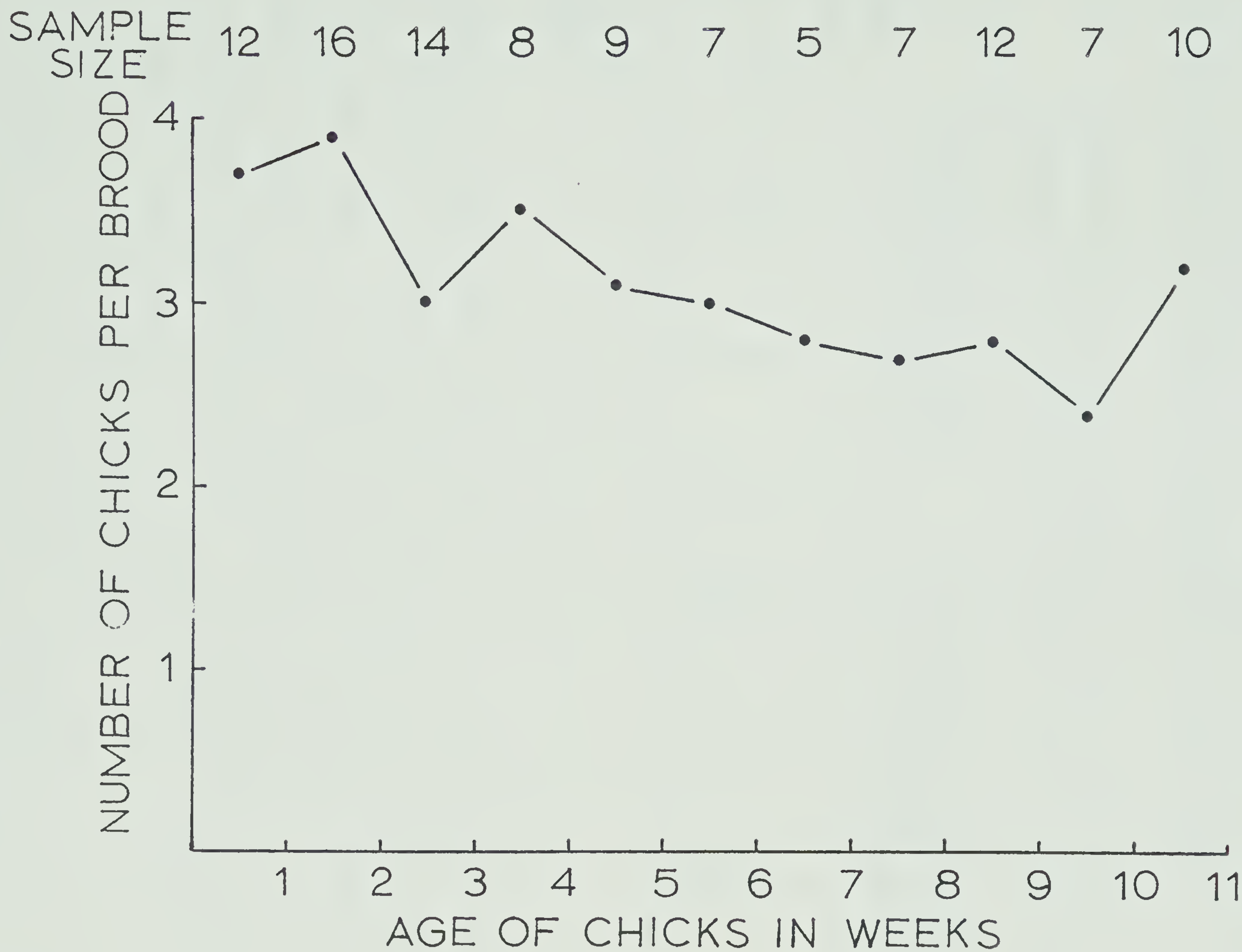
higher rate of disappearance than yearlings (difference was not statistically significant). Perhaps adults have a higher mortality rate than yearlings. Or perhaps the small sample sizes used have yielded misleading results.

Dispersalin Juveniles

The disappearance of chicks during summer is probably mainly equivalent to mortality. Some may leave the study area with the hen which raised them. The mortality rate of chicks during summer is probably highest during the first month of their lives as in the blue grouse (Bendell and Elliott, 1967). Figure 13 shows the average number of chicks per brood seen in all different broods seen at one week age intervals. Data for all four years are combined. From a high of 3.9 chicks per brood, this figure dropped to 3.1 chicks per brood by the end of the first month of life. This represents a mortality of approximately 20%. The true figure for mortality during the first month of life would be higher since mortality had probably already occurred in some broods before they were first observed. In addition, it was not always easy to accurately count the numbers of chicks per brood when they were young. Only minimum figures were used. By the time the chicks were 10 or 11 weeks of age, an average of about 2.9 (average of the data for the tenth and eleventh week) chicks remained in each brood.

In order to evaluate the disappearance of juveniles over their first winter, only banded juveniles were considered.

Figure 13. Average number of chicks seen per brood calculated for each week during the four summers of my study. The numbers above each point on the graph represent the numbers of broods seen each week.


SAMPLE SIZE
12 16 14 8 9 7 5 7 12 7 10
NUMBER OF CHICKS PER BROOD
4
3
2
1
1 2 3 4 5 6 7 8 9 10 11
AGE OF CHICKS IN WEEKS

Juveniles which were banded but were not present at a subsequent observation of the brood were assumed dead and are not included. All chicks banded were at least one month old. Table 39 shows the number of chicks seen on the study area as yearlings as well as the number of banded juveniles not seen again.

Table 39. Comparison of the fidelity of male and female juveniles to the study area over their first winter.

Year of Banding	Juveniles Seen Again on Study Area		Juveniles Not Seen Again on Study Area		
	F	M	F	M	Unknown Sex
1965	2	4	3	8	3
1966	3	8	11	5	
1967		1	15	4	9
Total	5	13	30	17	12

F = Female
M = Male

Table 39 shows that five out of 35 or 14% of the banded female juveniles present in the fall were seen on the study area the next year. In other words, 86% of them disappeared. The males, however, showed a much greater fidelity - 13 out of 30 or 43% stayed (57% disappeared). The difference in the proportions of the two sexes of juveniles which remained on the study area is statistically significant.

In addition to the five females seen again on the study area, one which was banded on the study area was seen 9,100 m from where banded. Another juvenile female was banded on the auxiliary study area and was seen again the next summer 9,100 m from where it was banded.

A comparison of distances moved by male and female chicks banded on the study area to another part of the study area is shown in Table 40.

Table 40. Comparison of distances moved by male and female chicks banded on the study area to another part of the study area the next year. Distances are measured from the centre of observations one year to the next year.

	Juvenile Females	Juvenile Males
Sample Size	5	13
Mean Distance Moved (m)	1,684	1,209
Range (m)	900-2,960	300-2,100
Standard Deviation (m)	868.6	625.7

The difference between the mean distance moved by male and female juveniles on the study area is not statistically significant.

The percentage of female and male juveniles resighted the following year is higher than for other species of grouse. Bendell and Elliott (1967) reported that out of 250 banded juvenile blue grouse, only 5 or 2% were resighted in subsequent years. Choate (1963) found that out of 150 banded white-tailed ptarmigan chicks, two females and 14 males returned to the area. Choate's findings that more male than female ptarmigan returned to the study area correspond to the results I found with spruce grouse.

In summarizing the above results, one could say that pro-

bably very few adults are involved in dispersal. Although some yearling females may emigrate from the study area, the main segment of the population involved in dispersal is the juvenile segment. Among the juveniles, females seem to disperse more widely than the males.

CONCLUDING SUMMARY

Dispersion and dispersal as well as several other aspects of the biology of female and young Franklin's grouse were studied in 1965-1968 on a 600 ha study area in southwestern Alberta.

A reliable technique for distinguishing adult from yearling females was developed using measurements of the diameter of the rachis and total length of the first primary, a central upper tail covert, and a central rectrix.

During four years of the study, approximately 37% of the spring population of females were yearlings. Nearly all new females entering the population were yearlings.

Yearling females appeared to use larger home ranges than adults. The longest dimension of the home range of yearlings was significantly larger than that of adults.

A technique for determining the age of juvenile Franklin's grouse was developed using measurements of their juvenal and postjuvenal primaries. Measurements of postjuvenal primaries could be used to estimate the ages of most juvenile Franklin's grouse to within two days, up to the age of eight weeks.

Using the technique for determining the age of juveniles, the chronology of reproductive events was determined. Most egg laying began between May 28 and June 11. During the four years of the study, 77% of the clutches hatched between June 28 and July 11. On the average approximately 50% of the females were successful at raising a brood. There was evidence that yearlings were not as successful at raising a brood as adults.

Females were rarely seen together. During spring, 30% of the females were with males whereas during summer, only 9% of females were with males. These results may be biased by a greater proportion of males to females being seen during the breeding period than during summer. However, I feel that this bias would not be sufficient to affect the finding that more females were with males during the breeding period than during the summer. Yearling females were not as closely associated with territorial males as were adult females. This is correlated with the indication that yearlings were not as successful at raising a brood as adults. It is possible that on the average, yearlings were not as mature or physiologically capable of reproduction as adults. Weights of yearlings taken in May were lower than those of adults. This may indicate that some yearling females were not sexually mature. In addition, the lower weight of females may preclude renesting attempts. It is also possible that the lower reproductive success of yearlings was related to aggressive behavior exhibited by females toward each other in the breeding period. Yearling

females, being new recruits, would possibly be at a disadvantage in establishing a home range near or coinciding with that of a territorial male if an adult female was already there. The result of this may be that some yearlings do not breed. Some evidence of this was found.

Although the study area included lodgepole pine (71.5%), the area), poplar and mixed forest (17.5%), relict spruce forest (3.5%), and meadow and marsh (7.5%), the majority of females were seen in 40% of the lodgepole pine forest. In the portion of the lodgepole pine forest inhabited by grouse, the average canopy coverage of overstory was greater and middlestory less, canopy height, diameter, and density of trees weregreater, and the slope of the terrain was less steep than in the unoccupied area.

Within the area of the lodgepole pine forest where females were found, they selected specific areas in terms of overstory and middlestory cover. The data indicated that yearling females did not select different cover than the adults. During the breeding period, females selected cover which was not very different from that which was present on the average over the area inhabited by females. At this time, females use the cover which is similar to that used by males (McLachlin, in prep.), probably because they are attracted to males. Females seen in summer with broods selected a relatively light overstory and a relatively heavy middlestory compared to that selected in the breeding period. This may reflect a dependence of young juveniles upon insects for protein. Females without broods seen in summer selected both a heavier overstory cover and a heavier

middlestory cover than during the breeding period. Females without broods selected a heavier overstory cover and lighter middlestory cover than females with broods. This preference for heavier cover may result from the possibility that during the moult birds are less capable of escaping from predators.

The data on dispersal showed that juveniles were the main segment of the female and juvenile population involved in dispersal. Of the banded female juveniles, 14% were seen on the study area in a subsequent year. Of the banded male juveniles, 43% were seen on the study area in a subsequent year.

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Appendix 1. Population estimate (P) of female Franklin's grouse on a study area in southwestern Alberta, 1965.

Date	A	B	C	AB	≤AB	≤C	P
May 22	1	0	0	-	-	-	-
May 26	1	1	0	1	1	-	-
June 21	1	2	0	2	3	-	-
June 22	1	3	1	3	6	1	6
July 12	1	3	0	3	9	1	9
July 21	1	4	1	4	13	2	7
July 22	1	4	1	4	17	3	6
July 23	1	4	0	4	21	3	7
July 25	1	5	1	5	26	4	7
July 26	1	5	0	5	31	4	8
July 27	2	6	2	12	43	6	7
July 30	1	6	0	6	49	6	8
July 31	1	7	1	7	56	7	8
Aug. 9	1	7	1	7	63	8	8
Aug. 11	2	7	2	14	77	10	8
Aug. 14	1	7	1	7	84	11	8
Aug. 18	1	7	1	7	91	12	8
Aug. 22	1	7	0	7	98	12	8
Aug. 27	2	8	1	16	114	13	9
Aug. 30	4	9	3	36	150	16	9
Sept. 4	2	10	1	20	170	17	10
Sept. 5	2	11	0	22	192	17	11
Sept. 8	2	13	2	26	218	19	11

A = numbers of grouse seen on any date
B = number of marked grouse present on the study area on any date
C = number of marked grouse seen on any date

For any estimate (P), the numbers substituted for A,B,C, must represent data for which the date is the same.

Appendix 2. Population estimate (P) of female Franklin's grouse on a study area in southwestern Alberta, 1966.

Date	A	B	C	AB	≶AB	≶C	P
May 2	1	11	0	11	11	0	-
May 11	1	12	0	12	23	0	-
May 16	1	13	0	13	36	0	-
May 17	3	14	0	42	78	0	-
May 18	1	17	1	17	95	1	95
May 21	1	17	1	17	112	2	56
May 23	1	17	0	17	129	2	65
May 24	1	18	1	18	147	3	49
May 28	1	18	1	18	165	4	41
May 31	1	18	1	18	183	5	37
June 1	5	18	4	90	273	9	30
June 5	1	19	0	19	292	9	32
June 6	2	20	2	40	332	11	30
June 8	1	20	0	20	352	11	32
June 17	1	21	1	21	373	12	31
June 19	2	21	2	42	415	14	30
June 21	1	21	1	21	436	15	29
June 29	1	21	1	21	457	16	29
July 6	3	21	3	63	520	19	27
July 7	3	21	2	63	583	21	28
July 13	1	22	1	22	605	22	28
July 14	4	22	3	88	693	25	28
July 15	3	23	3	69	762	28	27
July 16	2	23	2	46	808	30	27
July 18	2	23	2	46	854	32	27
July 19	3	23	2	69	923	34	27
July 20	1	24	1	24	947	35	27
July 21	3	24	2	72	1,019	37	28
July 22	1	25	1	25	1,044	38	27
July 26	4	25	3	100	1,144	41	28
July 30	1	26	1	26	1,170	42	28
Aug. 2	3	26	3	78	1,248	45	28
Aug. 3	1	26	1	26	1,274	46	28
Aug. 8	1	26	1	26	1,300	47	28
Aug. 9	3	26	3	78	1,378	50	28
Aug. 10	1	26	1	26	1,404	51	28
Aug. 11	3	26	3	78	1,482	54	27
Aug. 13	2	26	2	52	1,534	56	27
Aug. 14	3	26	3	78	1,612	59	27
Aug. 15	1	26	1	26	1,638	60	27
Aug. 16	3	26	3	78	1,716	63	27
Aug. 17	2	26	2	52	1,768	65	27
Aug. 18	1	26	1	26	1,794	66	27

Appendix 2 continued.

Date	A	B	C	AB	≤AB	≤C	P
Aug 20	1	26	1	26	1,820	67	27
Aug 21	2	26	2	52	1,872	69	27
Aug 22	4	26	3	104	1,976	72	27
Aug 23	1	27	1	27	2,003	73	27
Aug 25	1	27	1	27	2,030	74	27
Aug 28	4	27	4	108	2,138	78	27
Sept 1	5	27	5	135	2,273	83	27
Sept 2	1	27	1	27	2,300	84	27
Sept 3	2	27	2	54	2,354	86	27
Sept 4	3	27	1	81	2,435	87	28
Sept 7	3	29	3	87	2,522	90	28
Sept 13	5	29	5	145	2,667	95	28

A = numbers of grouse seen on any date
B = number of marked grouse present on the study area on any date
C = number of marked grouse seen on any date

For any estimate (P), the numbers substituted for A, B, C, must represent data for which the date is the same.

Appendix 3. Population estimate (P) of female Franklin's grouse on a study area in southwestern Alberta, 1967.

Date	A	B	C	AB	ΣAB	ΣC	P
May 17	1	19	1	19	19	1	19
May 21	1	19	1	19	38	2	19
May 22	2	19	1	38	76	3	25
May 23	1	20	1	20	96	4	24
May 27	3	20	2	60	156	6	26
May 28	2	21	2	42	198	8	25
May 29	1	21	1	21	219	9	24
June 1	7	21	6	147	366	15	24
June 2	3	22	3	66	432	18	24
June 4	1	22	1	22	454	19	24
June 5	2	22	1	44	498	20	25
June 6	1	23	1	23	521	21	25
June 8	3	23	2	69	590	23	26
June 14	1	24	1	24	614	24	26
June 17	1	24	1	24	638	25	26
June 22	1	24	1	24	662	26	25
June 23	1	24	1	24	686	27	25
June 25	1	24	0	24	710	27	26
June 26	1	25	1	25	735	28	26
July 9	2	25	1	50	785	29	27
July 11	1	26	1	26	811	30	27
July 12	1	26	1	26	837	31	27
July 14	2	26	1	52	889	32	28
July 15	2	27	2	54	943	34	28
July 20	1	27	1	27	970	35	28
July 22	1	27	1	27	997	36	28
July 24	2	27	2	54	1,051	38	28
July 27	2	27	2	54	1,105	40	28
Aug. 1	1	27	0	27	1,132	40	28
Aug. 9	1	28	1	28	1,160	41	28
Aug. 12	2	28	2	56	1,216	43	28
Aug. 20	1	28	1	28	1,244	44	28
Sept. 5	1	28	0	28	1,272	44	29
Sept. 8	2	29	2	58	1,330	46	29
Sept. 10	2	29	2	58	1,388	48	29
Sept. 12	2	29	1	58	1,446	49	30
Sept. 13	3	30	3	90	1,536	52	30

A = numbers of grouse seen on any date
B = number of marked grouse present on study area on any date
C = number of marked grouse seen on any date

For any estimate (P), the numbers substituted for A, B, C, must represent data for which the date is the same.

Appendix 4. Population estimate (P) of female Franklin's grouse on a study area in southwestern Alberta, 1968.

Date	A	B	C	AB	≤AB	≤C	P
May 5	2	17	0	34	34	0	-
May 7	2	19	2	38	72	2	36
May 10	1	19	1	19	91	3	30
May 16	5	19	3	95	186	6	31
May 17	2	21	1	42	228	7	33
May 18	4	22	1	88	316	8	40
May 21	1	25	1	25	341	9	38
May 22	1	25	1	25	366	10	37
May 23	2	25	1	50	416	11	38
May 25	2	26	2	52	468	13	36
May 26	3	26	3	78	546	16	34
May 27	1	26	1	26	572	17	34
May 28	1	26	1	26	598	18	33
June 8	3	26	2	78	676	20	34
June 11	3	27	3	81	757	23	33
June 12	2	27	2	54	811	25	32
June 13	4	27	4	108	919	29	32
June 14	2	27	2	54	973	31	31
July 4	1	27	1	27	1,000	32	31
July 8	4	27	4	108	1,108	36	31
July 10	6	27	5	162	1,270	41	31
July 11	4	28	1	112	1,382	42	33
July 14	1	31	1	31	1,413	43	33
July 15	1	31	1	31	1,444	44	33
July 16	1	31	1	31	1,475	45	33
July 25	1	31	1	31	1,506	46	33
July 29	1	31	1	31	1,537	47	33
July 31	2	31	2	62	1,599	49	33
Aug. 10	1	31	1	31	1,630	50	33
Aug. 24	1	31	0	31	1,661	50	33

A = numbers of grouse seen on any date
B = number of marked grouse present on the study area on any date
C = number of marked grouse seen on any date

For any estimate (P), the numbers substituted for A, B, C, must represent data for which the date is the same.

Appendix 5. Number of cover values for individual and combined species in the overstory and middlestory on 114 random plots within lodgepole pine forest in the area where grouse were not found.

Cover value *	Species: *Picea glauca*	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix* sp.	*Alnus crispa*	*Betula glandulosa*	*Potentilla fruticosa*	*Rosa* sp.	*Shepherdia canadensis*	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	2	-	-	-	-	-	-	-	-	4
4	-	7	-	-	-	-	-	-	-	-	11
3	2	41	-	-	-	-	-	-	-	-	38
2	14	52	1	1	1	-	-	-	-	-	51
1	44	11	3	1	19	-	-	-	-	-	9
0	54	1	110	112	94	-	-	-	-	-	1
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	2	-	-	-	-	4
3	1	-	1	-	1	8	-	-	-	-	20
2	3	1	-	2	10	21	2	1	1	5	34
1	39	20	4	7	50	28	-	1	16	7	45
0	71	93	109	105	53	55	112	112	97	102	11

* 6 = >95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present - 5%, 0 = absent.

Appendix 6. Number of cover values for individual and combined species in the overstory and middlestory on 111 random plots within lodgepole pine forest in the area where grouse were found.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	1	-	-	-	-	-	-	-	-	1
4	-	35	-	-	-	-	-	-	-	-	42
3	-	52	-	-	-	-	-	-	-	-	51
2	15	18	-	1	-	-	-	-	-	-	16
1	45	4	2	1	35	-	-	-	-	-	1
0	51	1	109	109	76	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	1	-	-	-	-	2
3	-	-	-	-	1	2	-	-	-	-	5
2	2	2	-	-	6	11	-	-	-	-	29
1	48	12	3	7	76	28	1	1	16	7	68
0	61	97	108	104	28	69	110	110	95	104	7

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present -5%, 0= absent.

Appendix 7. Number of cover values for individual and combined species in the overstory and middlestory on 56 plots where adult females were seen during the breeding period.

Cover value *	Species										Total
	Picea glauca	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix* sp.	*Alnus crispa*	*Betula glandulosa*	*Potentilla fruticosa*	*Rosa* sp.	*Shepherdia canadensis*	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	3	-	-	-	-	-	-	-	-	8
4	-	17	-	-	-	-	-	-	-	-	18
3	-	23	-	-	2	-	-	-	-	-	20
2	8	10	3	-	7	-	-	-	-	-	9
1	13	3	4	3	16	-	-	-	-	-	1
0	35	-	49	53	31	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	2	1	-	-	-	-	5
2	2	-	-	-	9	5	-	-	-	2	20
1	28	4	2	2	31	15	1	7	13	9	29
0	26	52	54	54	14	35	55	49	43	45	2

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present -5%, 0 = absent.

Appendix 8. Number of cover values for individual and combined species in the overstory and middlestory on 24 plots where yearling females were seen during the breeding period.

Cover value *	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	3	-	-	-	-	-	-	-	-	3
4	-	7	-	-	-	-	-	-	-	-	10
3	1	7	-	-	-	-	-	-	-	-	6
2	3	6	-	-	2	-	-	-	-	-	5
1	11	1	-	2	9	-	-	-	-	-	-
0	9	-	24	22	13	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	1	-	-	-	-	-	1
2	2	-	-	-	2	1	-	-	-	-	8
1	13	4	-	3	14	12	-	-	3	-	15
0	9	20	24	21	7	11	24	24	21	24	-

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 = >5-25%, 1 = present - 5%, 0 = absent.

Appendix 9. Number of cover values for individual and combined species in the overstory and middlestory on 80 plots where adult and yearling females were seen during the breeding period.

Cover value *	Picea glauca	Pinus con-torta	Populus balsam-ifera	Populus tremu-loides	Salix sp.	Alnus crispa	Betula gland-ulosa	Poten-tilla fruti-cosa	Rosa sp	Shep-herdia cana-densis	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	6	-	-	-	-	-	-	-	-	11
4	-	24	-	-	-	-	-	-	-	-	28
3	11	30	-	-	2	-	-	-	-	-	26
2	24	16	3	9	9	-	-	-	-	-	14
1	44	4	4	5	25	-	-	-	-	-	1
0		-	73	75	44	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	3	1	-	-	-	-	6
2	4	-	-	-	11	6	-	-	-	2	28
1	41	8	2	5	45	27	1	7	16	9	44
0	35	72	78	75	21	46	79	73	64	69	2

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present - 5%, 0 = absent.

Appendix 10. Number of cover values for individual and combined species in the overstory and middlestory on 70 plots where adult females with broods were seen during the summer.

Cover value *	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	13	-	1	-	-	-	-	-	-	19
3	1	30	2	-	1	-	-	-	-	-	33
2	11	20	2	1	3	-	-	-	-	-	17
1	24	2	5	6	11	-	-	-	-	-	1
0	34	5	61	62	55	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	3	-	-	-	-	-	5
4	-	-	-	-	8	-	-	-	-	-	16
3	-	-	-	-	20	2	1	-	-	1	19
2	4	2	5	2	17	2	2	8	-	5	22
1	45	13	8	18	15	21	4	15	29	18	7
0	21	55	57	50	7	45	63	47	41	46	1

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 = > 5-25%, 1 = present - 5%, 0 = absent.

Appendix 11. Number of cover values for individual and combined species in the overstory and middlestory on 23 plots where yearling females with broods were seen during summer.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	1	-	-	-	-	-	-	-	-	1
4	-	2	-	1	-	-	-	-	-	-	3
3	-	9	-	-	-	-	-	-	-	-	9
2	1	4	-	-	1	-	-	-	-	-	6
1	15	6	2	-	1	-	-	-	-	-	4
0	7	1	21	22	21	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	1
4	-	-	-	-	1	-	-	-	-	-	1
3	-	-	-	-	8	1	-	-	-	-	9
2	1	-	-	1	2	2	-	-	-	-	6
1	11	6	1	6	7	5	1	3	8	7	6
0	11	17	22	16	5	15	22	20	15	16	-

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present - 5%, 0 = absent.

Appendix 12. Number of cover values for individual and combined species in the overstory and middlestory on 110 plots where adult and yearling females with broods were seen during the summer.

Cover value *	Species										Total
	Picea glauca	Pinus con-torta	Populus balsam-ifera	Populus tremu-loides	Salix sp.	Alnus crispa	Betula gland-ulosa	Poten-tilla fruti-cosa	Rosa sp.	Shep-herdia cana-densis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	2	-	-	-	-	-	-	-	-	2
4	-	20	-	2	-	-	-	-	-	-	27
3	1	45	2	-	1	-	-	-	-	-	48
2	13	27	2	1	4	-	-	-	-	-	27
1	46	10	8	6	14	-	-	-	-	-	6
0	50	6	98	101	91	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	3	-	-	-	-	-	6
4	-	-	-	-	9	-	-	-	-	-	19
3	-	-	-	-	31	3	1	-	-	1	34
2	5	3	5	4	24	5	2	8	1	7	31
1	67	24	11	29	28	32	5	20	42	26	18
0	38	83	94	77	15	70	102	82	67	76	2

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5-25%, 1 = present -5%, 0 = absent.

Appendix 13. Number of cover values for individual and combined species in the overstory and middlestory on 19 plots where adult females without broods were seen during the summer.

Cover value *	*Picea glauca*	*Pinus contorta*	*Populus balsamifera*	*Populus tremuloides*	*Salix* sp.	*Alnus crispa*	*Betula glandulosa*	*Potentilla fruticosa*	*Rosa* sp.	*Shepherdia canadensis*	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	1	-	-	-	-	-	-	-	-	3
4	-	15	-	-	-	-	-	-	-	-	14
3	-	3	-	-	-	-	-	-	-	-	2
2	-	-	-	-	2	-	-	-	-	-	-
1	11	-	-	-	2	-	-	-	-	-	-
0	8	-	19	19	15	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	1	-	-	-	-	-	2
3	-	-	-	-	1	1	-	-	-	-	4
2	2	-	-	-	4	4	-	-	-	-	5
1	7	4	-	1	7	5	-	1	2	2	4
0	10	15	19	18	6	9	19	18	17	17	4

* 6 =>95-100%, 5 =>75-95%, 4 =>50=75%, 3 =>25-50%, 2 =>5 -25%, 1 = present - 5%, 0 = absent.

Appendix 14. Number of cover values for individual and combined species in the overstory and middlestory on 17 plots where yearling females without broods were seen during the summer.

Cover value *	Species										Total
	Picea glauca	Pinus contorta	Populus balsamifera	Populus tremuloides	Salix sp.	Alnus crispa	Betula glandulosa	Potentilla fruticosa	Rosa sp.	Shepherdia canadensis	
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	1	-	-	-	-	-	-	-	-	4
4	1	3	1	-	-	-	-	-	-	-	4
3	1	7	1	-	-	-	-	-	-	-	8
2	4	5	1	-	1	-	-	-	-	-	1
1	7	-	1	1	3	-	-	-	-	-	-
0	4	1	13	16	13	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	1
4	-	-	-	-	1	-	-	-	-	-	1
3	-	-	-	-	3	-	-	-	-	-	7
2	1	-	1	-	6	2	1	-	3	-	4
1	8	1	2	5	6	4	1	1	3	6	4
0	8	16	14	12	1	11	15	16	11	11	-

* 6 =>95-100%, 5 =>75-95%, 4 =>50=75%, 3 =>25-50%, 2 =>5-25%, 1 = present -5%, 0= absent.

Appendix 15. Number of cover values for individual and combined species in the overstory and and middlestory on 46 plots where adult and yearling females without broods were seen during the summer.

Cover value *	Picea glauca	Pinus con-torta	Populus balsam-ifera	Populus tremu-loides	Salix sp.	Alnus crispa	Betula gland-ulosa	Poten-tilla fruti-cosa	Rosa sp.	Shep-herdia cana-densis	Total
Overstory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	3	-	-	-	-	-	-	-	-	8
4	1	20	1	-	-	-	-	-	-	-	22
3	1	16	1	-	-	-	-	-	-	-	15
2	6	6	1	1	3	-	-	-	-	-	1
1	21	-	2	1	9	-	-	-	-	-	-
0	17	1	41	44	34	-	-	-	-	-	-
Middlestory											
6	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	1
4	-	-	-	-	2	-	-	-	-	-	3
3	-	-	-	-	7	1	-	-	-	-	14
2	4	1	1	-	10	6	1	-	3	-	11
1	22	7	3	8	19	11	2	3	8	8	13
0	20	38	42	38	8	28	43	43	35	38	4

* 6 =>95-100%, 5 =>75-95%, 4 =>50-75%, 3 =>25-50%, 2 =>5 -25%, 1 = present -5%, 0 = absent.